University of Alberta

Movement and fertilization success of American Redstarts (*Setophaga ruticilla*) in a fragmented agricultural landscape

by

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Abstract

Males of many passerine species make off-territory movements to pursue extra-pair fertilizations. Male off-territory movement investment should depend on the likelihood of paternity gain (extra-pair fertilizations) and loss (cuckoldry). Habitat fragmentation may influence fertilization success by reducing conspecific density and functional connectivity of the landscape. I studied American Redstart (*Setophaga ruticilla*) movement and fertilization success within breeding clusters in a fragmented agricultural landscape in Meanook, Alberta. Extra-pair paternity was higher in high-breeding-density years (54% of broods) than in low-breeding-density years (17% of broods). High-quality males, with many local females, in highly forested clusters invested most in movement. In the high-breeding-density years these males cuckolded low-quality, late-arriving males at the periphery of these clusters and in isolated clusters. Cuckoldry was equally likely in all clusters, yet only males in highly forested clusters with many local females achieved extra-pair fertilizations. Since males benefit highly from extra-pair fertilizations they may avoid settling in isolated clusters.

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TABLE OF CONTENTS

CHAPTER 1: THESIS INTRODUCTION 1

LITERATURE CITED 2

CHAPTER 2: TIMING OF BREEDING, MALE QUALITY AND TERRITORY-CONTEXT INFLUENCE FERTILIZATION SUCCESS OF AMERICAN REDSTARTS (*SETOPHAGA RUTICILLA*) IN A FRAGMENTED AGRICULTURAL LANDSCAPE 3

INTRODUCTION 3

METHODS 4

Study site and weather conditions 4

Correlates of extra-pair fertilization success 5

Genetic Analysis 7

Statistical Analysis 10

RESULTS 11

Study-population attributes 11

Parentage analysis 12

Fertilization success 13

DISCUSSION 17

Attributes of cuckolded males 18

Attributes of males that achieved EPFs 18

Differences in patterns of cuckoldry and EPF success: isolated males 20

Annual changes in EPF rates 21

LITERATURE CITED 22

CHAPTER 3: MALE QUALITY AND TERRITORY-CONTEXT INFLUENCE OFF-TERRITORY MOVEMENT OF AMERICAN REDSTARTS (*SETOPHAGA RUTICILLA*) IN A FRAGMENTED AGRICULTURAL LANDSCAPE 26

INTRODUCTION 26

METHODS 28

Study site and study population 28

General methods 29

Genetic Analysis 29

Radio-telemetry 29

Analysis of tracking locations and territory boundaries 30

Correlates of movement investment 32

Spatial autocorrelation 33
Statistical Analysis 33
RESULTS 34
Effects of Radio-transmitters 34
Movement patterns 35
Correlates of movement investment (paired males) 38
Movement and fertilization success 41
DISCUSSION 41
Why move? 41
When to move? 42
Who moves? 43
Why moving males did not achieve extra-pair fertilizations 45
Why the relationship between movement and EPF success should not be ruled out 47
LITERATURE CITED 47

CHAPTER 4: GENERAL DISCUSSION 51

FUTURE STUDY 51
LITERATURE CITED 53

APPENDIX 2-1. TERRITORY DISTRIBUTION, CUCKOLDRY AND EPF SUCCESS FROM 2003 TO 2005 54

APPENDIX 2-2. BREEDING SYNCHRONY INDICES 57

APPENDIX 2-3. PCR REACTION CONDITIONS AND MICROSATELLITE CHARACTERISTICS 58

APPENDIX 2-4. WEATHER CONDITIONS 59

APPENDIX 2-5. "SYNCHRONY" MODELS OF FERTILIZATION SUCCESS 60

APPENDIX 3-1. 2004 ACTIVITY SPACES AND TERRITORY DISTRIBUTION 61

APPENDIX 3-2. RADIO-TRANSMITTER ATTACHMENT AND RETRIEVAL METHOD 62

APPENDIX 3-3. ERROR IN BIRD LOCATIONS 63

APPENDIX 3-4. SPATIAL AUTOCORRELATION 64

APPENDIX 3-5. MOVEMENT INVESTMENT BY BREEDING STAGE AND TRACKING TIME-CATEGORY 65

LIST OF TABLES

TABLE 2-1. CHARACTERISTICS OF MICROSATELLITE LOCI FOR PATERNITY ANALYSIS WITH 2002 AND 2003 AMERICAN REDSTART POPULATIONS 8

TABLE 2-2. AMERICAN REDSTART STUDY-POPULATION ATTRIBUTES FROM 2002 TO 2005. 12

TABLE 2-3. SIMULATION PARAMETERS AND RESULTS OF *CERVUS* LIKELIHOOD PARENTAGE ANALYSIS ON 2002-2005 REDSTART POPULATIONS. 13

TABLE 2-4. GENERALIZED LINEAR MODELS OF CUCKOLDRY AND EXTRA-PAIR FERTILIZATION SUCCESS FOR INDIVIDUAL MALES AND WITHIN CLUSTERS FOR 2002 AND 2003 REDSTART POPULATIONS. 15

TABLE 3-1. MULTIPLE LINEAR REGRESSION MODELS FOR MALE OTM FREQUENCY, INTRUSION FREQUENCY AND PERCENT TIME OFF-TERRITORY. 40

TABLE 2-3-1. REACTION CONDITIONS AND THERMAL PROFILES FOR PCR AMPLIFICATION OF MICROSATELLITES USED IN PARENTAGE ANALYSIS. 58

TABLE 2-3-2. CHARACTERISTICS OF MICROSATELLITE LOCI FOR PATERNITY ANALYSIS WITH 2004 AND 2005 AMERICAN REDSTART POPULATIONS.. 58

TABLE 2-5-1. "SYNCHRONY" GENERALIZED LINEAR MODELS OF CUCKOLDRY AND EXTRA-PAIR FERTILIZATION SUCCESS FOR INDIVIDUAL MALES AND WITHIN CLUSTERS FOR 2002 AND 2003 REDSTART POPULATIONS.. 60

TABLE 3-4-1. MORAN'S I AND GETIS-ORD GENERAL G TESTS FOR SPATIAL AUTOCORRELATION IN ARCGIS 9.0 WITH DEPENDENT MOVEMENT INVESTMENT VARIABLES AT VARIOUS THRESHOLD DISTANCES. 64

TABLE 3-5-1. OTM FREQUENCY, INTRUSION FREQUENCY AND PERCENT TIME OFF-TERRITORY FOR 19 PAIRED MALES RELATIVE TO BREEDING STAGE OF THE SOCIAL MATE AND TRACKING TIME-CATEGORY. 65

LIST OF FIGURES

FIGURE 2-1. 2002 TERRITORY DISTRIBUTION, CUCKOLDRY AND EPF SUCCESS IN THE STUDY SITE NEAR ATHABASCA, AB. 14

FIGURE 2-2. EXTRA-PAIR FERTILIZATION SUCCESS AT THE CLUSTER-LEVEL AND BY PAIRED MALES RELATIVE TO THE TOTAL NUMBER OF FEMALES IN A CLUSTER, OR WITHIN A 200M RADIUS OF A PARTICULAR MALE, RESPECTIVELY 17

FIGURE 3-1. ACTIVITY SPACES FOR 8 MALES TRACKED IN 2003. 36

FIGURE 3-2. PERCENTAGE OF INTRUSIONS ONTO THE TERRITORY OF FEMALES AT EACH BREEDING STAGE... 37

FIGURE 3-3. INTRUSIONS BY SY MALES ONTO TERRITORIES OF SY AND ASY MALES. 38

FIGURE 2-1-1. 2003 TERRITORY DISTRIBUTION, CUCKOLDRY AND EPF SUCCESS IN THE STUDY SITE NEAR ATHABASCA, AB.. 54

FIGURE 2-1-2. 2004 TERRITORY DISTRIBUTION, CUCKOLDRY AND EPF SUCCESS IN THE STUDY SITE NEAR ATHABASCA, AB.. 55

FIGURE 2-1-3. 2005 TERRITORY DISTRIBUTION, CUCKOLDRY AND EPF SUCCESS IN THE STUDY SITE NEAR ATHABASCA, AB.. 56

FIGURE 2-4-1. MEAN MONTHLY TEMPERATURE (°C) BEFORE (APRIL AND MAY) AND DURING (JUNE) THE PEAK NESTING PERIOD OF REDSTARTS IN THE STUDY LANDSCAPE FROM 2002 THROUGH 2005.. 59

FIGURE 2-4-2. TOTAL PRECIPITATION (MM) BEFORE (APRIL AND MAY) AND DURING (JUNE) THE PEAK NESTING PERIOD OF REDSTARTS IN THE STUDY LANDSCAPE FROM 2002 THROUGH 2005. 59

FIGURE 3-1-1. ACTIVITY SPACES FOR 13 MALES TRACKED IN 2004. 61

FIGURE 3-3-1. ERROR IN BIRD LOCATIONS.. 63

Chapter 1: Thesis Introduction

Over 70% of socially monogamous avian species are genetically promiscuous (Griffith et al., 2002) and both males and females may devote a considerable portion of the breeding season to finding and attracting extra-pair mates (Westneat and Stewart, 2003). Behavioural studies have shown that territory-boundaries are highly permeable, in many species, and that home ranges can be up to an order of magnitude larger than breeding territories (e.g. Naguib et al., 2001). Many studies have focussed on how mating systems and male and female characteristics (e.g. behaviour, phenotypic and genetic quality) influence the opportunity for extra-pair paternity (EPP), and the role EPP plays in shaping mating systems and driving sexual selection (e.g. sexual dichromatism; Møller and Birkhead, 1994; the expression of elaborate male traits such as song and bright plumage, Ligon 1999). However, given the extent of human-induced habitat loss and fragmentation in temperate breeding areas, surprisingly few studies have assessed how the landscape structure and composition might influence extra-pair behaviour.

Habitat loss and fragmentation should influence the costs and benefits of pursuing extra-pair fertilizations (EPFs) by influencing the distribution of mates in the landscape and the ability or willingness to access them. For example, reduced forest cover and increased isolation of forest patches may decrease conspecific density and increase the costs or perceived risks of movement (Desrochers and Hannon, 1997; Grubb and Doherty, 1999).

I studied American Redstarts (*Setophaga ruticilla*) in a fragmented agricultural landscape near the Meanook Biological Research Station. Redstarts are Neotropical migrants that breed from late May to early July and during this time there is an intense flurry of nesting activity, off-territory movement and extra-pair interactions. In the study landscape, redstart populations have been monitored since 1998 as part of a long-term demographic study (Hannon, unpublished) and have declined from 2002 to 2005 (see Chapter 2). I assessed the relationship between movement and EPF success and how this is influenced by male attributes, timing of breeding, and characteristics of the study landscape (breeding density and forest cover). In chapter 2, I assessed patterns and correlates of cuckoldry and EPF success from 2002 to 2005. I was fortunate enough to

have over 600 DNA samples across two high-breeding-density and two low-breeding-density years which allowed me to assess the impact of density on fertilization success across years. There was also a gradient of breeding densities across the study landscape, which allowed an investigation of the effect of density on fertilization success within years. In chapter 3, I looked at patterns and correlates of investment in off-territory movement by radio-tracked males, whether or not this corroborated fertilization success patterns, and what this tells us about the role of males and females and the landscape in mediating fertilization success. In the final discussion I end with some important and interesting questions to pursue in future studies.

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Chapter 2: Timing of breeding, male quality and territory-context influence fertilization success of American Redstarts (*Setophaga ruticilla*) in a fragmented agricultural landscape

Introduction

The major benefit of extra-pair fertilizations (EPFs) for males of most bird species is an increase in reproductive success (Birkhead and Møller, 1992). Although EPFs occur in most passerine species (Griffith et al., 2002), the factors influencing variation in EPF success are poorly understood (Petrie and Kempenaers, 1998). This is likely because EPFs are the result of complex interactions between attributes of individuals, timing of breeding, and ecological factors. Furthermore, the conditions which promote or hinder EPF success may differ among populations and years (Westneat and Sherman, 1997). Therefore, a male's ability to achieve EPFs likely depends on a suite of factors operating at multiple spatial and temporal scales.

Old males (Perreault et al., 1997, Kleven et al., 2005) and males in better body condition (e.g. Dyrcz et al., 2005) often sire more within and extra-pair young. Unpaired males (Webster et al., 2001) and polygynous males (Hamao and Saito, 2005) often sire fewer extra-pair young than monogamous males. Increased breeding density can increase EPF rates (review in Westneat and Sherman, 1997; Thusius et al., 2001; Charmantier and Perret, 2004; but see Dunn et al., 1994; Tarof et al., 1998; and Ratti et al., 2001) because of increased encounters between extra-pair mates, reduced time and energy costs of finding mates (Birkhead and Møller, 1992) or an increased ability of females to assess male quality and thereby choose a high quality extra-pair mate (assuming females engage in EPFs to obtain high quality genes; Birkhead and Møller, 1992; Sullivan, 1994).

Since male display intensity (e.g. aggression or song output) may vary across nest stages, high breeding synchrony may standardize the context of male displays allowing females to more easily detect and choose high-quality extra-pair mates (Stutchbury and Morton, 1995; Stutchbury, 1998), thereby increasing EPF rates. However, high synchrony could reduce EPF rates if males face a strong trade-off between protecting within-pair paternity and pursuing EPFs (Westneat et al., 1988; see also Stutchbury, 1998, and Weatherhead and Yezerinac, 1998). If males do experience a trade-off, early

arriving males whose mates nest earlier (Dyrcz et al., 2005) should be cuckolded less and achieve more EPFs since they can intrude on fertile females when their own mate is no longer fertile.

EPF rates may also be influenced by habitat fragmentation (e.g. reduced patch size and increased isolation, Fahrig, 2003). Reduced forest cover could decrease conspecific density and increase the costs or perceived risks of movement (Grubb and Doherty, 1999). Encounter rates may be reduced because of decreased connectivity between neighbours (i.e. increased distance and unfavourable intervening matrix-type), and lower patch occupancy (Norris and Stutchbury, 2001).

In this study, I assess inter and intra-annual predictors of fertilization success (i.e. cuckoldry and EPF success) for male American Redstarts (*Setophaga ruticilla*) breeding in mature forest in an agricultural matrix in central Alberta. Redstarts are sexually dichromatic Neotropical migrants. They engage in a mixed reproductive strategy with high frequencies of extra-pair broods (59%, Perreault et al., 1997; 64%, Kappes, 2004) and polyterritorial polygyny (4-30%, Perreault et al., 1997, Secunda and Sherry, 1991). My objectives were to 1) describe patterns of fertilization success for males in two high-population-density and two low-population-density years, and 2) determine correlates of fertilization success in relation to timing of breeding (nest initiation date and breeding synchrony), male attributes, mating status, breeding density and forest cover. I predicted that high-quality males (older and in better body condition) would arrive earlier, nest earlier, and therefore be less frequently cuckolded and more likely to achieve EPFs. I also predicted that males with a greater availability of and access to fertile mates (in high density areas and years, and in high forest cover) and less cost to pursuing EPFs (low synchrony) would have high within-pair and extra-pair fertilization success.

Methods

Study site and weather conditions

The study was conducted from May through July 2002 to 2005 in forest fragments within a 10km^2 radius of the Meanook Biological Research Station (54°37'N, 113°20'W; Figure 2-1), near Athabasca, Alberta, Canada. Aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), conifer (white spruce, *Picea glauca*; black spruce,

Picea mariana; tamarack larch, *Larix laricina*) and mixtures of these cover approximately 40% of the landscape. Some forest patches are connected by fencerows along field edges. The remainder of the landscape contains agricultural fields, livestock grazing areas, farmyards, residences and roads. Within aspen woodlots, redstarts breed in cluster of wet, dense and structurally heterogeneous stands of willow (*Salix* spp.) and alder (*Alnus* spp.).

Since 1998, territory boundaries of all males in 17 breeding clusters were mapped and digitized (Hannon, unpublished data). I defined breeding habitat as any area covered by a territory in more than one season and created a polygon shapefile around all breeding habitat to delineate the cluster boundary. Used habitat that was farther than the mean territory width of territories of monogamous radio-tracked males (~100m; unpublished data) from the nearest used habitat was considered to be a separate cluster (Figure 2-1, and Appendix 2-1).

Since weather conditions may also influence EPF rates (Johnsen and Lifjeld, 2006), I determined mean monthly temperatures and total precipitation before (April) and during (May and June) the peak nesting period, across years. Data were obtained from the Colinton, Alberta weather station which is approximately 4km northeast of the study landscape (54°63'N, 113°22'W; Environmeat Canada).

Correlates of extra-pair fertilization success

Age, body condition and breeding parameters

Most males were captured within two weeks of arrival using mistnets, playbacks of conspecific song and a mounted redstart dummy. We measured body mass and non-flattened wing chord, attached coloured leg-bands and a CWS metal leg-band and took a blood sample for DNA analysis (see below). Plumage attributes (males) and shape and colour of retrices (females, Pyle 1997) were used to classify birds as SY (second year) or ASY (after-second year). Male mass was determined using a digital balance and measured to the nearest 0.1 g, and wing chord was measured to the nearest 0.1 cm. Using a generalized linear model (GLM; Poisson errors) I calculated a "body condition index" (BCI) by pooling years and regressing male mass on capture date and wing length (a surrogate of structural size) with age-category as a factor (SY or ASY; Sockman and Schwabl, 2001). The resulting residuals were not significantly different across years

(ANOVA: F=1.21, df=3, 116, p=0.31) and increasingly positive and negative residuals represented males in better and poorer condition, respectively (Robb et al., 1992). As part of a long-term demographic study (Hannon, unpublished) nests were located and territories were visited every two days to assess mating status (unpaired, monogamous or polygynous), breeding stage, clutch sizes and to confirm the identity of pair-fathers by observing feeding at nests.

Breeding density, breeding synchrony and forest cover

ArcGIS 9.0 (ESRI, 2004) was used for all spatial analyses. Aerial photos from 2003 (1:20,000) were geo-referenced with 1:50,000 Alberta Base Features, and digitized to create a landscape coverage classified into forest, agriculture, water, and anthropogenic features (i.e. roads, human residences and buildings). The minimum mapping unit was approximately 5 x 5m. Male territories determined via spot mapping were scanned and digitized into GIS and territory centroids were found using the *mean center* function in ArcMap.

I considered local density and local synchrony to be independent for neighbouring males (as Tarof et al., 1998; Thusius et al., 2001; Charmantier and Perret, 2004; Estep et al., 2005) since these values could vary extensively within a cluster. "Local female density" was defined as the number of females in territories that (at least partially) fell within a 200m radius of the territory centroid of each paired male. Cluster-level female density was the number of females within the area (ha) encompassed by a polygon drawn around all territories in a cluster.

The female fertile period was considered to be from five days before the first egg was laid until the day the penultimate egg was laid (Perreault et al., 1997). Local, cluster-level and population-level breeding synchrony were calculated using the breeding synchrony index of Kempenaers (1993; Appendix 2-2) modified to consider the number of available females within a 200m radius, within the breeding cluster or within the study population, respectively (Appendix 2-2). Percent forest cover varied little for males within the same cluster, so only cluster-level forest cover was measured. The cluster-level female-density polygon was buffered by 200m and the percent forest was calculated within this expanded polygon.

Genetic Analysis

Template DNA collection and extraction

Nest predation and parasitism by brown-headed cowbirds (*Molothrus ater*) prevented complete genetic sampling (cowbirds may eject redstart eggs and kill redstart chicks, unpublished), but sampling effort was similar across years (2002: 53% of 220 laid eggs, 2003: 63% of 176, 2004: 63% of 99, 62% of 117; χ^2=6.97, df=3, p=0.07). Between 25 and 50 µl of blood was collected from the brachial vein of adults and six-day old nestlings, stored in Queen's lysis buffer (Seutin et al., 1991) and refrigerated at 4°C for up to a year until extraction. Most extractions were conducted using QIAGEN DNeasy® Tissue Kits (Qiagen Inc.). Tissue was also prepared from 38 chicks that died during rainstorms and 39 unhatched eggs using QIAGEN DNeasy® Tissue Kits (Qiagen Inc.) and following specialized protocols for avian blood and tissue (Bush et al., 2005). Template DNA concentration from all extractions ranged between 50 and 250 ng/µl. All extracted samples were stored at -20°C for up to one year until used.

Microsatellite screening

DNA was amplified via polymerase chain reaction (PCR) with a 5' fluorescent dye on either the forward or reverse primers, under conditions optimized specifically for each primer used (Appendix 1-3). Six di-nucleotide-repeat-motif microsatellite primers, developed for use in other songbird species, were screened for use. Loci were highly polymorphic ranging from 7-19 alleles and had high heterozygosity (Table 2-1, and Appendix 2-3). All loci were checked for deviations from Hardy-Weinberg equilibrium with GenePop on the Web (Raymond and Rousset, 1996) independently for each year using all adults in the study population each season. I conducted the heterozygote deficiency test (one-tailed; Table 2-1 and Appendix 2-3). Only *Dpµ* 03 in 2002 showed a significant heterozygote deficiency after a Bonferroni adjustment for multiple tests (24 tests, adjusted alpha=0.002; Webster et al. 2004), but since it was highly polymorphic and deficient in only one year, it was used in analyses.

Table 2-1. Characteristics of microsatellite loci for paternity analysis with 2002 and 2003 American Redstart populations (2004 and 2005 were similar; Appendix 2-3). Values were calculated from the adult population in each year.

Locus	Reference	Size range (bp)	Year	Number of alleles	Heterozygosity $h_{observed}$	Heterozygosity $h_{expected}$	Exclusion probability (both parents known)	Null frequency
Dpu 03	Dawson et al. (1997)	132-178	2002	12	0.441	0.582[a]	0.380	0.1494
			2003	7	0.500	0.481	0.289	0.0468
Cup 04	Gibbs et al. (1999)	154-194	2002	16	0.892	0.894	0.633	-0.0019
			2003	16	0.886	0.870	0.731	-0.0129
Dpu 16	Dawson et al. (1997)	148-182	2002	16	0.871	0.887	0.620	0.0070
			2003	16	0.943	0.898	0.784	-0.0291
Mau 23	Alderson et al. (1999)	142-156	2002	7	0.765	0.720	0.535	0.0282
			2003	8	0.784	0.762	0.534	-0.0185
Dca 28	Webster et al. (2001)	174-218	2002	18	0.791	0.819	0.672	0.0227
			2003	17	0.807	0.870	0.743	0.0380
Dca 32	Webster et al. (2001)	218-256	2002	14	0.914	0.881	0.753	-0.0238
			2003	13	0.864	0.875	0.743	0.0380
Average			2002	13.83			0.998[b]	
			2003	12.83			0.999[b]	

[a] denotes a statistically significant heterozygote deficiency (after a Bonferroni adjustment for multiple tests; adjusted α=0.002) based on the procedure by Rousset and Raymond (1995), calculated in *Cervus*.
[b] Average probability of paternal exclusion: the probability that a random non-sire male from the population will not possess the paternal allele found in the offspring, given that the maternal genotype is known.

Running samples

A home-made size standard was run in each lane to enable allele sizing. Samples were run on polyacrylamide gels on an ABI Prism® 377 DNA sequencer, data were collected with GeneScan® Analysis Software (Applied Biosystems, 2001) and then analysed with Genotyper® software (Applied Biosystems, 2001). Samples that could not be scored the first time were re-run. Similarly, samples with allele sizes that did not conform to the expected di-nucleotide-repeat motif (e.g. an allele of 163bp when 162bp and 164bp were expected) were re-run to confirm their consistency.

Paternity assignment

I used the program *Cervus* 2.0 (Marshall et al., 1998), which assigns parentage to offspring using a likelihood approach, rather than strict exclusion (i.e. where young are excluded based on a certain number of mismatches with putative fathers). The likelihood method is a more realistic approach to paternity assignment since it incorporates information about allele frequencies, incomplete sampling of candidate sires, missing genotypes and mismatches caused by mis-typing, null-alleles and microsatellite mutation (Marshall et al., 1998). It ranks putative fathers by the likelihood that they are the true

father relative to other males in the population. It then calculates a delta value which is the difference in likelihood between the most likely and next most likely males.

Simulation parameters

The number of unsampled males was estimated from the number of males known to be unsampled with an allowance of two additional unsampled males in each year (i.e potential floaters or males residing beyond the study population boundaries). I assumed that all chicks were offspring of their social mother and so the error rate used in analyses was estimated from the number of mismatches between mothers and chicks (Marshall et al., 1998). I expected that if chicks were descended from their social mother they should show few allelic mismatches, but if they were the result of intra-specific brood parasitism I expected to see multiple mismatches (Webster et al., 2004). Few chicks mismatched their social mother at two or more loci (3, 2, 0 and 5 offspring in 2002 to 2005, respectively) and I assumed these to be potential incidences of brood parasitism or mixed or mislabeled samples. When multiple chicks mismatched the mother at the same locus, I counted this as one mismatch and adjusted the genotyping error rate accordingly. I used the same error rate in simulations as in likelihood calculations (see results). I chose to assign paternity at the *Cervus* default levels of 95% and 80%.

Re-assignments

I modified a portion of *Cervus* assignments, similar to the "total evidence" approach of Webster et al. (2004). If the most likely father mismatched the chick at 2 or more loci, I assumed that the true father was not among the pool of candidate males and was therefore unsampled (since double errors within one genotype should be rare). A lower ranking male with fewer mismatches than the most likely male was assigned as the true sire, if delta values were similar. To reduce Type I error (i.e. H_o: pair father is the true father), when two males matched a chick at all loci, and the pair father was one of them, the pair father was assigned paternity. A sire was not assigned if two non-pair-fathers had the same number of mismatches. Re-assignments reduced the number of extra-pair young detected in most years, but most re-assignments occurred with 80% confidence assignments when delta values were low (Webster et al., 2004). Furthermore, *Cervus* assignments and my assignments never found statistically different levels of extra-pair broods or young (see results).

Statistical Analysis

Across years, offspring in two nests were sampled for each of seven polygynous males and for each of 4 pairs who re-nested. Since the costs and benefits of EPFs may be different for each nesting event, and since the number of males with two nests was small in each year (2-4), I included both nests in all cases. An average of 29% and 18% of males and females were present in consecutive years, and four males and females were present in three years. However, only three males paired with the same female in two study years and in only one case did the pair have sampled offspring in both years (2002 and 2003). This pair was included in both years.

All statistical analyses were carried out in S-Plus (Insightful Corp., 2005). Univariate comparisons used parametric tests and all dependent variables were tested for normality (Kolmogorov-Smirnov goodness of fit test) and equality of variances when appropriate. Chi-square goodness of fit tests were conducted using Yates' continuity correction when appropriate (Zar, 1999). All tests are two-tailed and all means are reported ± 1 standard error. I used a significance level of 0.05 for all univariate tests and considered relationships with $0.05<p\leq0.1$ as trends in the data.

I modeled male fertilization success using cuckoldry (no, yes) and EPF success (no, yes) as dependent variables (GLM with binomial errors; Crawley, 2002). I pooled years and included the terms *year, arrival,* date of first egg (*DFE*), male age category (*age*), male body condition index (*BCI*), mating status (*status;* for cuckoldry: monogamous or polygynous, for EPF success: unpaired, monogamous or polygynous) and local density of females (*local density*). DFEs were earlier in 2003 (Julian dates: $\bar{x}_{2002}=166\pm1.4$, min=155, n=37 nests; $\bar{x}_{2003}=162\pm1.2$, min=151, n= 43 nests; day 151= May 31st) so I increased 2002 values by 4 days to enable comparison among years (following this transformation, DFE distribution did not differ by year: t=-0.01, p=0.99). The first males arrived at similar times in each year (2002=140, 2003=141), but arrival date distribution differed ($\bar{x}_{2002}=150\pm0.66$, n=57 males; $\bar{x}_{2003}=147\pm0.54$, n= 46; t=3.75, $p<0.01$) and could not be transformed so I included a *year x arrival* interaction term in models. I also included a *year x density* term to test for different effects of density in each year.

I also ran cluster-level models to assess whether the proportion of males cuckolded or achieving EPFs in a cluster was related to *year*, cluster-level density (*cluster density*) and forest-cover (*forest cover*; GLM with binomial errors; Crawley, 2002). I included a *cluster density x forest cover* interaction since density and forest cover may interact to influence movement and therefore fertilization success. Small sample size at the cluster-level precluded including a *year x density* term.

In all models, including synchrony would have excluded males in isolated clusters with no neighbours (since these males had no local or cluster-level synchrony value assigned). To assess the effects of synchrony, I also ran the above models including *synchrony* at each scale. In these "*synchrony*" models I included a *density x synchrony* interaction term since density and synchrony may interact to influence fertilization success (Thusius et al., 2001).

To evaluate models, I used the *Step* function in S-Plus which iteratively adds and drops terms to find the most parsimonious model, given the specified terms, based on the *AIC* (Akaike Information Criterion) statistic (shown as the *Cp* statistic in S-Plus; S-Plus Guide to Statistics, 2001). In this process, terms are retained if they lower the model *AIC*. I considered any terms retained by this process to be important predictors of the dependent variables.

Results

Study-population attributes

There was a decrease in population abundance across years and the average local density of females, although similar between 2002 and 2003 and between 2004 and 2005 (post-hoc comparisons), was significantly greater in the first two years (χ^2= 23.14, df=3, p<0.01; Table 2-2). Across years, ASY males arrived earlier (t=2.10, df=101, p=0.04) than did SY males. The percentage of males that were ASY decreased across years (χ^2= 32.23, df=3, p<0.01) and the percentage of males that were polygynous increased in 2004 and 2005 (χ^2= 12.23, df=3, p=0.01; Table 2-2). There were no significant differences in male body condition (F=1.21, df=3, 116, p=0.31), the percentage of females that were ASY (χ^2= 0.45, df=3, p=0.93) nor the operational sex ratio (percent males, χ^2= 0.66, df=3, p=0.88) across years (Table 2-2). Population breeding synchrony was similar in

most years, but was lower in 2003 than in 2004 (χ^2=13.1, df=3, p<0.01). There were no significant trends in mean monthly temperature or total precipitation across years in May and June (when birds arrive and most females are fertile), although April was increasingly warmer and drier across years (Appendix 2-4).

Table 2-2. American Redstart study-population attributes from 2002 to 2005.

	Clusters occupied[a]		Abundance[b]		Average local density[c]	Operational sex ratio[d]	Percent ASY (#classified[e])		Percent UP:M:P[f]	Population Breeding synchrony[g]
	male	female	Male	Female			male	female		
2002	14	14	62	53	3.57±0.24	1.2	87	68 (41)	19:75:6	43± 2%
2003	15	14	53	44	3.08±0.31	1.2	62	75 (39)	23:77:0	36± 2%
2004	11	11	28	30	2.00±0.25	0.9	57	70 (23)	11:71:18	46± 3%
2005	11	11	27	24	1.95±0.18	1.1	26	74 (19)	30:51:19	41± 3%

[a] By breeding females and territorial (paired and unpaired) males; the total number of clusters was 17
[b] Number of breeding females; number of territorial plus known floater/non-resident males
[c] Average number of breeding females within a 200m radius of the territory centroid of each male
[d] Average number of males per female
[e] All males were aged; not all females were captured and a portion of captured females were not confidently aged
[f] Percentage of unpaired, monogamous, and polygynous males; total number of males given in the abundance column
[g] The average percentage of females fertile on a given day during the period when females in the population are fertile (Kempenaers, 1993; see methods); often late May to early July

Parentage analysis

Success of parentage analysis was greatest in 2003 and 2004 likely because a greater proportion of males were sampled in these years compared to 2002 and 2005. However, more than 75% of analysed offspring were assigned a sire in all years (Table 2-3). In each year, there was no significant difference between *Cervus* assignments and my assignments in terms of the percentage of extra-pair offspring (2002: χ^2=0.04, df=1, p=0.85; 2003: χ^2=1.00, df=1, p=0.32; 2004: χ^2=1.37, df=1, p=0.24; 2005: identical assignments; Table 2-3) and extra-pair broods (2002: χ^2<0.01, df=1, p>0.99; 2003: χ^2=1.31, df=1, p=0.25; 2004: χ^2=1.20, df=1, p=0.27; 2005: identical assignments; Table 2-3). Furthermore, across years, there was no significant difference in the percentage of extra-pair offspring I assigned with 80% and 95% confidence (80%: 23% of 94 offspring, 95%: 20% of 179 offspring; χ^2=0.34, df=1, p=0.56). Therefore, I conducted subsequent analyses using my assignments, and included young assigned at both 80% and 95% confidence.

Table 2-3. Simulation parameters and results of *Cervus* likelihood parentage analysis on 2002-2005 redstart populations.

		2002	2003	2004	2005
Sample details	percent of offspring sampled[a] (eggs laid)	53 (220)	63 (176)	63 (99)	62 (117)
	percent of samples analysed[b] (number)	92 (72)	88 (122)	92 (68)	79 (58)
Parentage analysis parameters and success rate	Candidate males[c] (percent sampled)	62 (87)	56 (91)	31 (91)	27 (78)
	percent loci typed	99.8	99.3	99.4	99.0
	average genotyping error rate[d]	0.030	0.018	0.023	0.022
	Cervus analysis success rate: 80%, 95%	74,33	100,74	97,59	88,45
	percent re-assigned[e]: 80%, 95%	6,0	21,1	16,0	0,0
	percent of analysed offspring assigned a sire (number)	71 (65)	95 (116)	96 (65)	76 (44)
	average number of assigned-offspring per sampled nest	2.3±0.2	2.9±0.2	3.2±0.3	3.1±0.3
Extra-pair paternity rates	percent extra-pair broods[f] (*Cervus*)	52 (56) n=27	56 (71) n=41	15 (35) n=20	19 (19) n=16
	percent extra-pair young[g] (*Cervus*)	28 (31) n=65	27 (34) n=116	6 (14) n=65	14 (14) n=44

[a] From nests of known clutch sizes; samples not obtained were lost through predation or parasitism by brown-headed cowbirds (*Molothrus ater*)
[b] Non-analysed offspring were young that mismatched their mother at ≥2 loci, or had one or both parents unsampled
[c] Known territorial and non-resident males, plus an allowance for 2 floater/non-resident males in each year
[d] Error rate adjusted for multiple-chick mismatches with mother (see methods)
[e] See methods for re-assignment criteria
[f] n=number of nests
[g] n=number of chicks

Fertilization success

In 2002 and 2003, an average of 28% of young were extra-pair and 54% of broods contained extra-pair young (2002 vs. 2003-young: χ^2=0.02, df=1, p=0.89; broods: χ^2=0.01, df=1, p=0.92) while in 2004 and 2005 an average of 10% of young were extra-pair and 17% of broods contained extra-pair young (2004 vs. 2005-young: χ^2=0.98, df=1, p=0.32; broods: χ^2=0.09, df=1, p=0.76; Table 2-3, Figure 2-1, and Appendix 2-1). The average rate of extra-pair paternity in 2002 and 2003 combined was higher than the average of 2004 and 2005 combined (young: χ^2=12.4, df=1, p<0.01; broods: χ^2=12.3, df=1, p<0.01).

A similar proportion of sampled males achieved EPFs across years (2002=11% of 54, 2003=22% of 51, 2004=7% of 28, 2005=13% of 24; χ^2=3.94, df=3, p=0.27). Across years, an average of 86% of males did not achieve EPFs, 6% achieved 1, 4% achieved 2, 3% achieved 3 and 1% achieved 4 EPFs. The mean distance between sires of extra-pair young and their extra-pair mates was 205±47m, and 92% of sires were less than 300m away. A total of 67% of sires were immediate neighbours, 79% were within two territories (but in the same cluster) and 21% were in a different cluster from their extra-

pair young. Of 5 males that sired young outside their resident cluster, 3 sired young in the nearest occupied cluster.

Levels of extra-pair paternity were high enough in 2002 and 2003, but not in 2004 and 2005, to allow multivariate analysis (Table 2-4). Although I was not able to assign paternity to all offspring in these years (Table 2-4), my ability to detect cuckoldry was not influenced by the number of offspring assigned per nest (binomial GLM: *cuckoldry (no,yes) ~year* x *number of offspring assigned*; no terms retained after *Step*), therefore, I used nests with different numbers of assigned young in analyses.

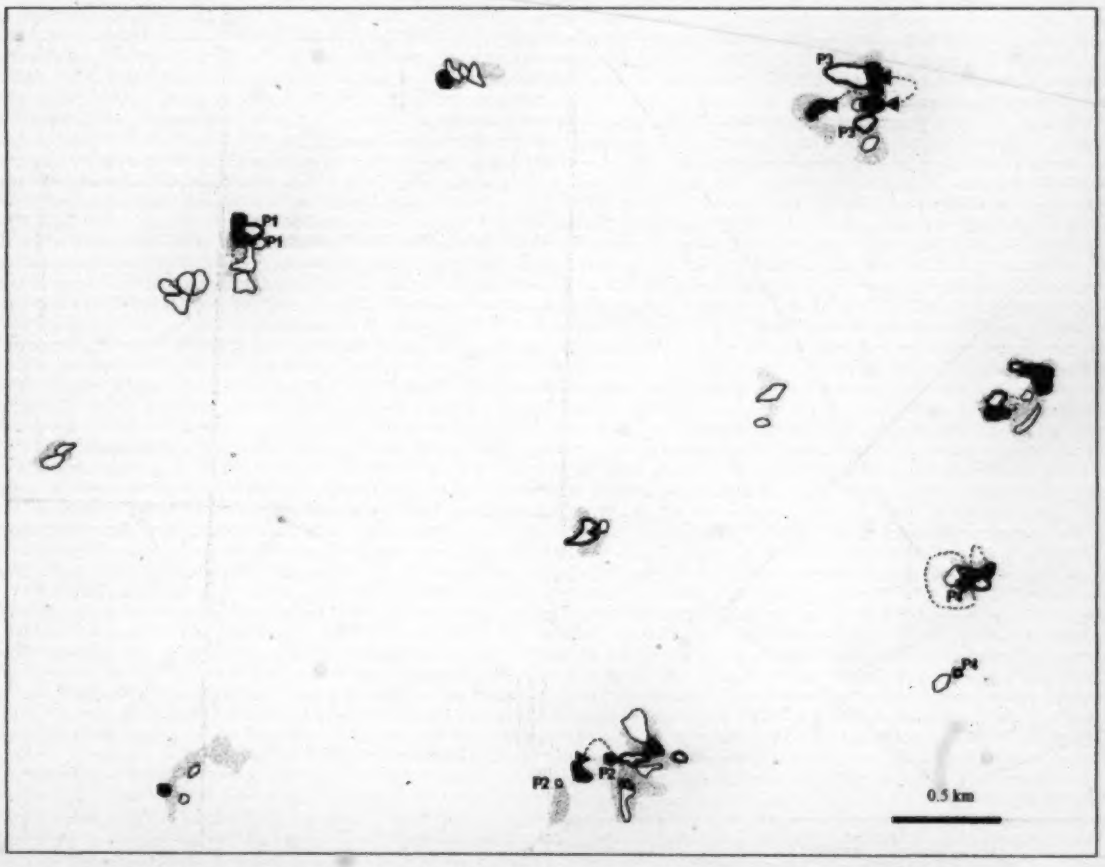

Figure 2-1. 2002 Territory distribution, cuckoldry and EPF success in the study site near Athabasca, AB. Light grey areas represent forest, white areas represent roads, fields and other non-habitat. Medium grey polygons represent breeding clusters (see methods). White polygons are territories of monogamous and polygynous ("P_n" for each territory) males. Thick black lines encircle territories where offspring were sampled. Dark grey identifies territories of cuckolded males, and dashed lines extend to the identified sire (but do not represent movement trajectories). Where both males were cuckolded, an arrow leads from the identified sire to the cuckolded male. (see Appendix 2-1 for 2003 to 2005 data).

Table 2-4. Generalized linear models of cuckoldry and extra-pair fertilization success for individual males and within clusters for 2002 and 2003 redstart populations. Terms were removed using the *step* function in S-Plus. A rank of removal of 1 indicates the term was first to be removed in the stepwise process and no rank indicates a term was retained. (See Appendix 2-5 for synchrony models).

Model	Coefficients[a]	χ^2 (df_{null}, $df_{residual}$)	p-value, direction of effect	Rank of removal	Percent Deviance explained by full model (by reduced model)
Male- Cuckolded? (no, yes)[b]					
Arrival	0.12	3.83	0.05 +		25 (24)
DFE	0.11	2.87	0.09 +		
Year x density	0.35	2.79	0.09 +		
BCI	1.09	2.18	0.14 -		
Year x arrival	0.20	0.72	0.39 -		
Density	0.32	0.71	0.40 -		
Year	28.45	0.70	0.40 +		
Age		0.92	0.34 +	2	
Status		0.55	0.46 -	1	
		(43, 34)			
Cluster- Proportion of males cuckolded[b]					
Density		1.80	0.18 +	4	14 (0)
Forest cover		1.15	0.28 +	3	
Density x forest cover		1.13	0.29 -	2	
Year		0.13	0.71 +	1	
		(23,19)			
Male – EPF achieved? (no, yes)[b]					
Density	0.30	2.06	0.15 +		25 (12)
Density x year	0.38	1.74	0.19 -		
Year	1.15	0.68	0.41 +		
BCI		1.83	0.18 -	5	
Arrival		0.66	0.42 -	4	
Year x arrival		0.18	0.67 +	3	
Age		2.05	0.15 +	2	
Status		1.67	0.43 -	1	
		(62,53)			
Cluster - Proportion of males achieving an EPF[b]					
Year	0.55	5.09	0.02 +		53 (53)
Density x forest cover	0.06	2.27	0.13 -		
Forest cover	0.11	2.19	0.14 +		
Density	5.70	1.84	0.17 +		
		(23,19)			

[a] coefficients are from reduced models (containing only retained terms)
[b] *GLM with binomial errors*

Cuckoldry

Cuckoldry was most likely for males in poorer body condition who arrived later (especially in 2002; *year* x *arrival* interaction, Table 2-4) and whose mates nested later in the season (i.e. later arriving females and re-nesting females) when synchrony was lowest (*DFE* vs. *local synchrony*: r= -0.51, n=71, p<0.01). Males surrounded by fewer local females were more likely to be cuckolded (especially in 2003; *year x density* interaction; Table 2-4). These males were either in small, isolated clusters with no other neighbours or peripheral males within less-isolated clusters with many other neighbours (Figure 2-1, and Appendix 2-1). At the cluster-level no terms were retained (Table 2-4), reflecting that an equal proportion of males were cuckolded in all clusters (Figure 2-1, Appendix 2-1).

EPF success

Although neither arrival time, age, mating status nor body condition alone predicted EPF success, a *post-hoc* model revealed a significant interaction between age and status (*age* x *status*: χ^2=10.11, n=122, p<0.01), indicating that monogamous ASY males were more likely to achieve an EPF than monogamous SY males (0% of 17 SY males and 15% of 87 ASY males).

Males with a high local density of females (especially in 2002; *year* x *density* interaction, Table 2-4) were most likely to achieve an EPF (Table 2-4). At the cluster-level a high proportion of males achieved an EPF in two types of clusters: 1) highly-forested clusters with a high density of females, and 2) highly-forested clusters with a low density of females (i.e. high female abundance but dispersed territories; *density* x *forest cover* interaction, Table 2-4). Although there were no significant non-linear relationships detected between density and EPF success at either scale (using spline fits in general additive models), there was a threshold effect on EPF success; EPFs were only achieved by males in clusters with 4 or more breeding females and only by males with 2 or more females within 200m (Figure 2-2).

Synchrony models

Males with lower local synchrony were most likely to be cuckolded, but cluster-level synchrony did not influence cuckoldry (Appendix 2-5). Males with high local synchrony (often males with early-nesting females) were most likely to achieve an EPF (Appendix 2-5). At the cluster-level a high proportion of males achieved EPFs in clusters with low cluster-level synchrony. The contrasting effects of synchrony on EPF success at each scale are reconciled in that, with the exception of two clusters, cluster-level synchrony was negatively related to female abundance (r=-0.53, n=15, p=0.04; i.e. clusters with more females were more likely to have at least some non-synchronous females). Therefore, males breeding in clusters with many females could be locally synchronous while cuckolding lower-synchrony cluster members.

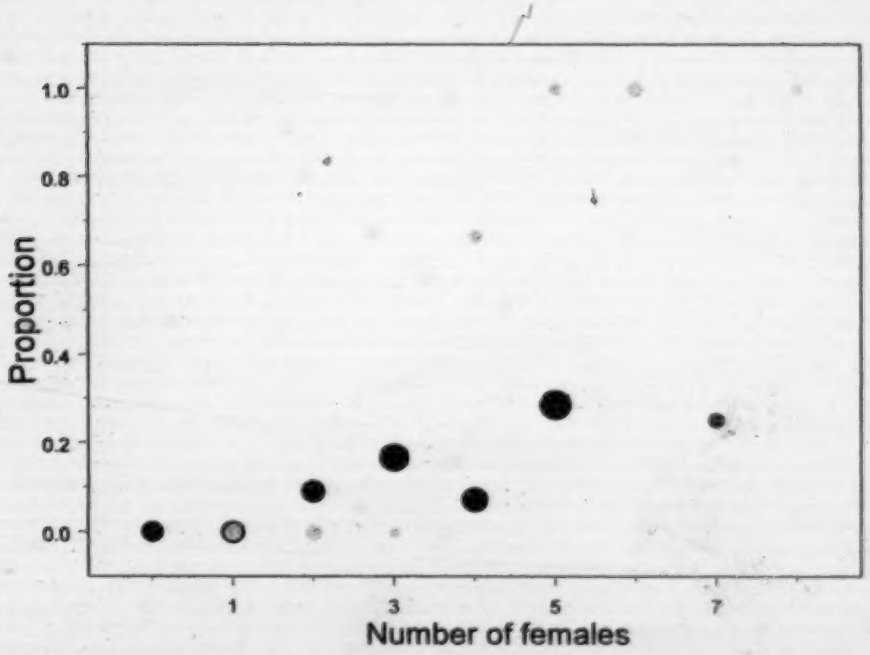

Figure 2-2. The proportion of clusters in which at least one EPF was achieved, relative to the number of females in a cluster (grey circles), and the proportion of males who achieved at least one EPF relative to the number of females within a 200m radius of a particular male (black circles). Circle size represents 1-6 sampled clusters (grey circles) and 4-21 sampled males (black circles).

Discussion

EPF patterns were similar to those found in many other passerines, where a few males sired the majority of extra-pair young, and most extra-pair sires cuckolded near neighbours within a few-hundred metres of their territory (e.g. Perreault et al., 1997; Stutchbury, 1998; Webster et al., 2001; Byers et al., 2004; although not Woolfenden et al., 2005). The distance between sires and their extra-pair young was similar to the range of male off-territory movements in 2003 and 2004 (90% of trips are within 200 m; Chapter 3). Interestingly, fertilization success varied extensively between high-breeding-density and low-breeding-density years. In 2002 and 2003, nearly one-third of young were extra-pair, while in 2004 and 2005 only about one-tenth of young were extra-pair, which is the lowest reported for redstarts to date (34-56%, Perreault et al., 1997; 24% and 52%, Kappes, 2004).

Attributes of cuckolded males

In the high-breeding-density years, males that arrived later, were in poorer body condition, settled in areas with fewer neighbours (i.e. in isolated clusters, or at the periphery of highly-forested clusters with many females) and were most likely to be cuckolded. These males paired with females who nested later, and thereby had low breeding synchrony right around their territories. Similarly, Tarof et al. (2005) found that Least Flycatcher (*Empidonax minimus*) males that arrived later were in poorer body condition, occupied territories at the periphery of breeding clusters, paired later and were more likely to be cuckolded. Late arriving males are disadvantaged in multiple ways. First, late-arriving males are of lower quality; late-arriving radio-tracked males showed a trend of having lower song rates in 2003 and 2004 than early-arriving males (unpublished data), and in other species late-arriving males have higher parasite loads (Dyrcz et al., 2005), smaller song repertoires and lower song versatility (Lampe and Espmark, 1994) and begin copulating later than early arriving males (Dyrcz et al., 2005). Second, since redstart males invest most in off-territory movement after the nest-building stage (Chapter 3), late-arriving males with late-nesting females (and therefore lower breeding synchrony) likely suffer more intrusions onto their territories while their mates are most fertile.

Contrary to my predictions, but consistent with a number of other studies, old and young males were equally likely to be cuckolded (Kempenaers et al., 1997; Tarof et al., 2005; Kleven et al., 2005). Likewise, males that achieve EPFs are often as likely to be cuckolded as males who do not achieve them (Kempenaers et al., 1997, Byers et al., 2004, Kleven et al., 2005). Polygynous males were not more likely to be cuckolded than monogamous males contrary to many studies suggesting that they are less able to guard multiple mates (Hamao and Saito, 2005, and references therein). However, only two of five polygynous males had paternity assigned in both nests during the high-density study years, so this should be examined further.

Attributes of males that achieved EPFs

In the high-breeding-density years, EPFs were achieved most frequently by ASY males (who arrived earlier than SY males) who settled in areas with more females (i.e. in clusters with many females and in central territories within clusters). These males paired

with females who nested earlier and thereby had high breeding synchrony with neighbours but low breeding synchrony in the cluster as a whole. Unpaired and floater SY males who held territories briefly, but likely roamed the landscape thereafter, also achieved a high number of EPFs (6).

As predicted, old paired males were highly likely to achieve EPFs, similar to many other species (Kempenaers et al., 1997; Perreault et al., 1997; Kleven et al., 2005). I found that old males invest most highly in off-territory movement (Chapter 3) but also that they were more likely to nest early (see below). Surprisingly, a high number of unpaired males achieved EPFs. Although unpaired males are often assumed to be of lower quality, they may successfully achieve EPFs in some years if females acquiesce to persistent harassment (Birkhead and Møller, 1992). Although not statistically significant, a lower proportion of polygynous males achieved EPFs (1 of 12) than monogamous males (13 of 104) reflecting their lower investment in pursuing EPFs (Chapter 3). Despite males in poorer body condition being more highly cuckolded, body condition was not a significant predictor of EPF success. Other male attributes such as song investment (Chapter 3) or plumage reflectance (Kappes, 2004; Estep et al., 2005) might be stronger predictors, but these characteristics were not measured for all males in my study.

While a number of studies have found no relationship between synchrony and fertilization success (e.g. Dunn et al., 1994; Perreault et al., 1997), Thusius et al. (2001) found that synchrony influenced cuckoldry, and that the direction of its effect was scale-dependent. Male Common Yellowthroats (*Geothlypis trichas*) with high local synchrony and low population synchrony were more likely to be cuckolded (Thusius et al., 2001). Interestingly, redstarts showed a similar pattern but with EPF success. Males with high local synchrony (i.e. early nesters, higher quality males) and low cluster-level synchrony (i.e. males in clusters with many females) frequently cuckolded asynchronous cluster members (peripheral and isolated, late-nesting, low-quality males). This suggests that early in the season, when local synchrony is high, males face a trade-off between guarding their mates (and thereby protecting within-pair paternity) and pursuing EPFs (Westneat et al., 1990). After the fertile period of their mate, males invest more in off-territory movement (Chapter 3), and correspondingly are more likely to achieve EPFs.

As predicted, in the high-density years, both forest cover and female density influenced fertilization success. Only males with more than two neighbours achieved

EPFs, and EPFs were only achieved by males in highly forested clusters with four or more breeding pairs. Tarof et al. (1998) suggested that in terms of access to extra-pair mates, a "search-cost" threshold may exist for some species, whereby dispersion of territories reduces EPF rates only when territories are very far apart. Therefore, at a certain level of territory dispersion either the cost of accessing neighbours outweighs male or female benefit (Tarof et al., 1998) or females cannot access enough males to adequately assess male quality (Westneat, 1990) and therefore EPF rates drop extensively. The apparent occurrence of a search-cost threshold for redstarts in this landscape may also help to explain differences among high and low-breeding-density years (see below).

Differences in patterns of cuckoldry and EPF success: isolated males

If only males from clusters with the highest density of females achieved EPFs, why did cuckoldry occur in both high and low-density clusters? In this landscape two types of males accessed isolated clusters: unpaired floating males, and old, high-quality males. First, in 2003, unpaired floating males who roamed the landscape cuckolded two males in isolated clusters. Second, high-quality ASY males invest the most in off-territory movement (Chapter 3), and accordingly, one high-quality ASY male (he had the highest song rate of radio-tracked males in the following year) from a cluster with a high density of females cuckolded a male in an isolated cluster. Therefore, although the majority of males are cuckolded by near neighbours, a few highly mobile males can access and cuckold isolated males who may arrive later, nest later and be of lower quality. Together these findings suggest that in this landscape ASY males should prefer highly forested clusters with a high density of females and other nearby clusters, where EPFs can balance or outweigh the high likelihood of cuckoldry. Interestingly, in this landscape SY males, who rarely achieve EPFs, frequently settle at the periphery of high-density clusters. Although SY males who breed in high-density clusters may lose reproductive success through cuckoldry, and not gain EPFs, they may also prefer these clusters if pairing success is more likely here (Birkhead and Møller, 1992; Tarof et al., 2005). However, a full assessment of the costs and benefits of settling in high and low-breeding-density clusters also requires consideration of factors that influence nest and

fledging success (e.g. food availability, inter-specific brood parasitism risk, and nest-predation risk).

Annual changes in EPF rates

A number of factors could be responsible for the decline in EPF rate across the four years of this study: a reduction in the proportion of ASY males, an increase in the proportion of polygynous males, declining habitat quality and decreasing breeding density. Since ASY males achieved nearly all EPFs in the high-density years, a decline in ASY males likely contributed to reduced EPF rates in 2004 and 2005. However, a 25% reduction in ASY males from 2002 to 2003 caused no change in EPF rate and with only a 5% reduction in ASY males from 2003 to 2004 the EPF rate dropped by about 75%. Mating status did not influence the likelihood of cuckoldry in the high-density years, so the increase in polygynous males alone should not have reduced EPF rates. However, eight of ten polygynous males in 2004 and 2005 were ASY males, which potentially reduced the number of ASY males seeking EPFs. Increasingly warmer and drier conditions in April could have decreased habitat quality (e.g. reduced food availability) which may have increased the relative costs of off-territory movement by males and thereby reduced encounter rates. However, movement investment by males in 2003 and 2004 was not different (Chapter 3), suggesting that habitat quality did not differ, or at least did not influence male encounter rates. However, the influence of habitat-quality on redstart EPF rates should be investigated more thoroughly. This leaves reduced breeding density as the most likely explanation for the decline in population-level EPF rates.

In many other studies, inter-population or inter-year differences in EPF rates correlate well with changes in population density (review in Westneat and Sherman, 1997; Charmantier and Perret, 2004). In 2004 and 2005, both population abundance and the average local density of females were significantly reduced (Table 2-2). Only about one-quarter of males had more than two neighbours, and only four clusters had four or more females in 2004 and 2005 respectively. Three of the five identified extra-pair sires from these years were residents of these high-breeding-density clusters. In the low-density years, a reduced EPF rate could have been the result of reduced encounter rates, higher costs of movement, or a reduced ability of females to assess male quality and thereby choose a high quality extra-pair mate (Sullivan, 1994). In 2003 and 2004, males

invested equally in off-territory movement (Chapter 3). However, female redstarts also engage in off-territory movements (personal observation) and in many species female movement is less frequent and more localised than for males (e.g. Norris and Stutchbury, 2002). Therefore, in low-density years, females may not encounter as many males if territories are dispersed. Also, if females engage in EPFs to obtain "good genes" they should only mate with a male they are confident is of higher quality than their social mate (Sullivan, 1994). Because there are fewer males in low-density years, females will receive fewer intrusions overall and thereby may have a reduced ability to assess and choose high quality mates (Sullivan, 1994).

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Chapter 3: Male quality and territory-context influence off-territory movement of American Redstarts (*Setophaga ruticilla*) in a fragmented agricultural landscape

Introduction

Movement of many male temperate-forest-breeding songbirds is not constrained by territory boundaries. Males may leave their territories for many reasons, including the expansion of territory boundaries (Birkhead and Møller, 1992), polyterrtorial polygyny (Secunda and Sherry, 1991), or the acquisition of public information (Doligez et al., 2002). The majority of off-territory movement (OTM) investment, however, is probably to pursue extra-pair copulations (EPCs; Hanski, 1992; Stutchbury, 1997; Naguib et al., 2001; Kleven et al., 2005; Woolfenden et al., 2005). The costs and benefits of OTMs are likely most related to paternity loss and gain (Birkhead and Møller, 1992), so the amount a male invests in OTMs should be based on his likelihood of gaining extra-pair fertilizations (EPFs) and losing within-pair fertilizations. Although many studies have assessed costs and benefits of male OTMs and correlates of fertilization success, there are few data on how movement investment directly relates to paternity gain and loss and how landscape structure influences fertilization success.

To achieve an EPF a male must successfully encounter, copulate with, inseminate and fertilise an extra-pair female (Westneat and Sherman, 1997). Therefore, the likelihood that a male gains an EPF should depend on the availability of and access to fertile extra-pair mates and, since females often choose extra-pair partners (Sullivan, 1994), male quality. Encounter rates may be increased by moving off-territory frequently (Kleven et al., 2005), and may be greater when the density of conspecifics is high (Stutchbury et al., 2005). The likelihood of achieving an EPF is increased if males visit fertile females (Stutchbury, 1998), and if males move when many females are fertile (i.e. high synchrony, Stutchbury et al., 1997). The primary cost to males of leaving their territories is cuckoldry (Birkhead and Møller, 1992), which may also be influenced by density, synchrony and male quality. When density and synchrony are high, a male may experience more intrusion onto his own territory. Thus moving off-territory when his mate is fertile may increase his probability of cuckoldry (Birkhead and Møller, 1992). However, females often prefer high quality mates (Kempenaers et al, 1992; Birkhead and

Møller, 1992; Ligon, 1999), so the benefit of movement is likely greater for high quality males. Accordingly, in some species older males (Kleven et al., 2005) and males with higher song investment (Naguib et al., 2001) invest the most in OTM, and often have greater within-pair and EPF success (Kempenaers et al., 1992; Perreault et al., 1997). Similarly, males in better body condition may sire more extra-pair young (Dyrcz et al., 2005).

The costs and benefits of movement may be different in fragmented than in continuous landscapes. Smaller patch size and increased isolation (Fahrig, 2003) may increase the costs of movement by reducing access to and availability of extra-pair mates. For example, in a fragmented landscape, smaller forest patches may support fewer conspecifics, they may be farther apart or access may be limited because of a reduced propensity to cross gaps (Desrochers and Hannon, 1997; Grubb and Doherty, 1999). Alternatively, if conspecific density is low, or dispersion of conspecifics is high, movement investment could increase in order to access additional females (e.g. Norris and Stutchbury, 2001). Finally, benefits of EPFs may be greater in fragmented landscapes with high levels of nest predation since EPFs may provide males with some reproductive success if their own nest is depredated (Perreault et al., 1997).

An agricultural landscape provides a good opportunity to assess the reproductive costs and benefits associated with movement. American Redstarts (*Setophaga ruticilla*) are sexually dichromatic Neotropical migrants. They engage in a mixed reproductive strategy with high frequencies of extra-pair broods (59%, Perreault et al., 1997; 64%, Kappes, 2004) and polyterritorial polygyny (4-30%, Perreault et al., 1997, Secunda and Sherry, 1991). Redstart male quality is related to age and song: older males with novel song types have higher pairing success, clutch sizes and fledging success (Lemon et al., 1992), and old males are most frequently sires of extra-pair and within-pair young (Perreault et al., 1997). In this study I report on OTMs and EPF success of American Redstarts breeding in mature forest embedded in an agricultural matrix in central Alberta. The objectives of this study were to 1) describe patterns of movement for males in this landscape at different temporal and spatial scales; 2) determine whether qualities of the male, the density and distribution of potential mates, and attributes of the landscape correlate with investment in movement; and 3) assess the costs and benefits of OTMs in this landscape in terms of within and extra-pair fertilization success. I predicted that high

quality males (older, higher song investment, better body condition) with greater availability and access to extra-pair mates (higher breeding density, higher forest cover and higher breeding synchrony) would leave their territories most frequently, intrude the most on other territories and spend the greatest amount of time off-territory. I also predicted that males that invested most in movement would be most successful at siring within and extra-pair young, since they would encounter extra-pair females most frequently, and because they would be higher quality males, and therefore preferred as mates by both within-pair and extra-pair females.

Methods

Study site and study population

The study was conducted from May through July 2003 and 2004 in forest fragments within a 10km^2 radius of the Meanook Biological Research Station (54°37'N, 113°20'W, Figure 3-1, Appendix 3-1), near Athabasca, Alberta, Canada. Aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), conifer (white spruce, *Picea glauca*; black spruce, *Picea mariana*; and larch, *Larix laricina*) and mixed-wood cover approximately 40% of the landscape. Some forest patches are connected by fencerows along field edges. The remainder of the landscape is comprised of agricultural fields, livestock grazing areas, farmyards, residences and roads. Within aspen woodlots, redstarts variably occupy 17 clusters of breeding habitat in wet, dense and structurally heterogeneous stands of willow (*Salix* spp.) and alder (*Alnus* spp.). Redstart abundance decreased from 2003 to 2004 (breeding females: 44 to 30; territorial males: 53 to 28), however, the relative distribution of females across clusters was similar between years (#females/cluster in 2003 vs. 2004, Spearman rank correlation: r_s=0.67, $n_{clusters}$=15, p=0.01), as was the age structure (proportion ASY males: 2003=0.62, 2004=0.57, χ^2=0.04, df=1, p=0.83; proportion ASY females: 2003=0.75, 2004=0.70, χ^2=0.01, df=1, p=0.91) and sex ratio (proportion males; 2003=0.54, 2004=0.48; proportions test: χ^2=0.29, df=1, p=0.59).

General methods

Males and females in the study landscape were captured using mistnets, playbacks of conspecific song, and a mounted redstart dummy. I attached coloured leg-bands and a CWS metal leg-band and took a blood sample for DNA analysis (see below). Plumage attributes (males) and shape and colour of retrices (females, Pyle 1997) were used to classify birds as SY or ASY. Male mass was determined using a digital balance and measured to the nearest 0.1 g, and non-flattened wing chord was measured to the nearest 0.1 cm. As part of a long-term demographic study (Hannon, unpublished) nests were located and territories were visited every two days to assess mating status (unpaired, monogamous or polygynous), breeding stage and clutch sizes.

Genetic Analysis

For a detailed description of genetic analyses see Chapter 2. A total of 333 samples were collected in 2003 and 2004 from 54 females, 66 males and 213 offspring (63% of all eggs laid). Between 25 and 50 µl of blood was collected from the brachial vein of adults and six-day old nestlings, stored in Queen's lysis buffer (Seutin et al., 1991). DNA was also extracted from tissue of 38 chicks that died during rainstorms and 33 unhatched eggs following specialised protocols for avian blood and tissue (Bush et al., 2005). I used six di-nucleotide-repeat-motif microsatellite primers with a high total exclusion probability (greater than 0.996 in each year). I used *Cervus* 2.0 (Marshall et al., 1998) to conduct paternity analyses using a likelihood approach.

Radio-telemetry

Radio-attachment

Eight and 14 different males were radio-tracked in 2003 and 2004 respectively. I attempted to choose paired males from clusters representing a range in local forest cover and densities of females. However, two males in 2003 and one in 2004 were unpaired. A 0.43g whip antenna radio-transmitter (LB-2N, Holohil Systems Ltd.) was attached using a gluing method modified from Raim (1978; Appendix 3-2). Tracked males weighed between 6.8 and 9.2 g, so radios represented 4.7-6.3% of body weight.

Tracking

Each male was tracked for 2h once every two to three days from either 6h00-8h00, 8h00-10h00, 10h00-12h00 or 14h00-16h00, across the breeding stages of his social mate (i.e. nest-building, laying, incubation and nestling), for the life of the transmitter battery (on average 14-21 days). If OTMs extended longer than the two-hour session, males were tracked until they returned to their territories. I typically followed males within 5 to 20m and locations, behaviours (e.g. chases, displays) and vocal status (i.e. singing, calling or silent) were recorded whenever males changed location or interacted with a predator or another bird. Breeding clusters had grid markers placed 25m apart and bird locations were estimated relative to the nearest grid point. When birds entered areas that had no grids, locations were marked with flags and their locations were later determined using a GPS. I accurately determined the position of a bird to within a 2.5m radius of its true location, providing I was within 30m of the bird (most locations). Since differentially corrected GPS points had a mean horizontal precision of about 2m, the location of each bird had a maximum error radius of about 4.5m (Appendix 3-3).

Analysis of tracking locations and territory boundaries

ArcGIS 9.0 (ESRI, 2004) was used for all spatial analysis. Aerial photos from 2003 (1:20,000) were georeferenced with 1:50,000 Alberta Base Features, and digitized to create a landscape coverage classified into forest, agriculture, water, and anthropogenic features (i.e. roads, human residences and buildings). The minimum mapping unit was approximately 5 x 5m. Tracking locations were plotted and converted to paths (Hawth's Tools; Beyer, 2004), and line lengths and distances from features were measured using the *measure* function in the editor toolbar. Activity space was calculated as the area within a minimum convex polygon (Hawth's Tools) of all tracking locations, and trip distance was net displacement from the territory edge.

Territory boundaries of all breeding pairs were estimated so that tracked males could be classified as on or off-territory. For non-radio-tracked males, territory boundaries were derived from locations of singing males taken about every two days until the nestling stage. Maps were scanned, georeferenced and digitized into GIS. I applied a 6m buffer inside territorial boundaries to account for location errors in the field.

If the nest of a breeding pair fell outside the inner 6m buffer, the unbuffered territory boundary was used for that pair.

For tracked males, territory boundaries were derived from plotting all singing locations in GIS excluding those that were within secondary territories (i.e. polyterritorial males). I used the *fixed kernel density estimator* in Hawth's Tools (h=25, percent volume contour=95) and removed points outside of this. A minimum convex polygon was then created and a 4.5m outer buffer was applied to account for the error in bird locations. Minimum convex polygons were chosen to define territory boundary lines, rather than kernel density contours, since singing locations of males generally enclose defended areas.

Cluster and patch boundaries

I defined breeding habitat as any area covered by a territory in more than one season based on territory maps compiled since 1998 (Hannon, unpublished data). Breeding clusters were defined as contiguous breeding habitat separated by at least 100m (mean territory width of territories of monogamous radio-tracked males) from other breeding habitat. A polygon shapefile was drawn around each cluster. A patch was considered to be any forested area disconnected from other forest by >30m, or connected to other forest by a corridor narrower than 30m. Redstarts have often been observed crossing roads, which are about 15m wide, and territories in this landscape are not always bounded by road edges. Therefore, males crossing roads were considered to be within the same patch.

Classifying movements

Movements were assessed at three scales. A movement outside the territory was considered an OTM. OTMs were then classified as to whether a male moved into unoccupied habitat, or onto the territory of other breeding pairs or unpaired males, which was an *intrusion*. If territories were separated by more than 20m, movement between these territories was considered movement into unoccupied habitat. Movements by males into unoccupied space within 20m of their territory boundary and not directed towards other territories were not considered in the OTM dataset since they likely reflect inaccuracies in boundary designations or variability in territory boundaries within and among days. Movement outside a breeding cluster was considered to be an *off-cluster*

movement, and any movement outside a forest patch was considered to be an *off-patch movement*. In 2004, both territories of three polygynous tracked males were adjacent, and males often sang while moving between them. Therefore, movements between these territories were not considered OTMs.

Correlates of movement investment

Age, mating status and body condition

Males were grouped by age category (ASY or SY), and by male minimum age based on returns of banded birds. SY males were classified as one year old and returning males banded the previous year as SYs and ASYs new to the study landscape were classified as two years old (Perreault et al. 1997). Returning males banded the previous year as ASYs, or two-years previous as SYs, were known to be three years old. These males were combined with one four-year-old to create a 3+ category. Males were either unpaired (n=3), monogamous (n=16) or polgynous (bigamous; n=3). I used a body condition index (BCI) calculated from males captured from 2002 to 2005 (Chapter 2). Using a generalized linear model (GLM; Poisson errors) I regressed male mass on capture date and wing length (a surrogate of structural size) with age-category as a factor (SY or ASY; Sockman and Schwabl, 2001). The resultant residuals did not differ between 2003 and 2004 (χ^2=0.93, n_{2003}=7, n_{2004}=14, p=0.35) and increasingly positive and negative residuals represent males in better and poorer condition, respectively (Robb et al., 1992).

Song investment

Male song was measured in two ways. In 2004, each time a territory was entered for nest monitoring, the number of songs per minute was averaged across three consecutive one-minute intervals. Males observed during the nestling stage, and on rainy days had lower song rates so these observations were omitted. For tracked males I also calculated the percent of on-territory locations where the male was recorded singing (only my tracking sessions). Sessions during the nestling stage, on rainy days, and with fewer than five total on-territory locations were omitted, and the mean percent on-territory singing locations/session was then calculated for each male.

Breeding synchrony

The fertile period of females was considered to be from five days before the first egg was laid until the day the penultimate egg was laid (Perreault et al., 1997). I calculated breeding synchrony as the average percentage of females fertile on a given day across the tracking period of a male within a 200m ("*synchrony 200*") and 500m ("*synchrony 500*") radius of a tracked male's territory centroid.

Landscape variables

"*Forest cover 200*" and "*forest cover 500*" variables were determined by calculating the amount of forest within 200m and 500m of territory centroids. Similarly, "*density 200*" and "*density 500*" were calculated as the number of breeding females in territories that at least partially fell within these radii.

Spatial autocorrelation

In 11 clusters one male was tracked but in four clusters multiple males were tracked. In two cases in 2004, two males from the same cluster were tracked, and in one case three males from the same cluster were tracked. In a fourth cluster, one male was tracked in 2003 and three males were tracked in 2004. Clustered observations may not be independent, therefore dependent variables were checked for spatial autocorrelation with years combined. There was no significant spatial autocorrelation in OTM frequency, intrusion frequency or percent time off-territory (ArcGIS; Moran's I: all $i<0.17$, all $p>0.1$; Getis-Ord General G: all $G<0.01$, all $p>0.1$; Appendix 3-4). Therefore, I chose to treat males as independent to increase sample sizes for multivariate tests. Furthermore, I also performed all statistical comparisons using mean values from each cluster, and results were not qualitatively different from those using all males individually.

Statistical Analysis

Univariate analysis

All statistical analyses were carried out in S-Plus (Insightful Corp., 2005). Dependent variables were tested for normality (Kolmogorov-Smirnov goodness of fit test) and equality of variances when appropriate. Non-normal dependent variables were transformed to normality when possible using log+1 transformations. Univariate comparisons used parametric tests, and Chi-square goodness of fit tests were conducted

using Yates' continuity correction when v=1. Correlation tests used Pearson's product-moment method when at least one variable was normal and Spearman's rank correlation when both were non-normal (Zar, 1999). All tests were two-tailed and means were reported ± 1 standard error. I used a significance level of 0.05 for all tests and considered relationships with $0.05<p\leq0.1$ as trends in the data.

Multivariate analysis

Multiple linear regression was carried out in S-Plus using the *lm* function. I ran separate models for dependent variables (OTM frequency, intrusion frequency and percent time off-territory) at each spatial scale (200m and 500m), including approximately 1/3 as many variables as the number of samples in a given model (Crawley, 2002). Each model contained *year*, body condition (*BCI*), *age (*minimum male age), and *song* (percent singing locations/session), *density* (200m or 500m), *synchrony* (200m or 500m) and *forest cover* (200m or 500m). I had no *a priori* expectations of which explanatory variables were most important, so I conducted stepwise regression using the *Step* function in S-Plus. *Step* iteratively adds and drops terms to find the most parsimonious model, given the specified terms, based on the *AIC* (Akaike Information Criterion) statistic (shown as the *Cp* statistic in S-Plus; S-Plus Guide to Statistics, 2001). In this process, terms are retained if they lower the model *AIC*. Because sample size was too low to test for interactions in global models, I tested whether a *forest cover x density* interaction improved each retained model since these factors might interact to influence movement investment. If this interaction term remained following stepwise selection it was reported.

Results

Effects of Radio-transmitters

Transmitters did not appear to influence male behaviour. Males fitted with transmitters resumed singing within 20 min post-release, engaged in typical complex aerial feeding manoeuvres and chases with other birds, remained paired and none died. Furthermore, in 2004, tracked males did not have different song rates (songs/min) than non-tracked males ($\bar{x}_{tracked}$=5.9±0.6, n=12, $\bar{x}_{non\text{-}tracked}$= 6.4± 1.2, songs/min, n=5; t=0.39, df=13, p=0.70). Mass at time of recapture for radio removal was available for five males

and increased in four and remained the same for the fifth. Finally, the return rate of tracked and non-tracked birds was similar following each study year (2004 returns: 25% of 8 tracked, 26% of 43 non-tracked, $\chi^2<0.01$, df=1, p=0.97; 2005 returns: 21% of 14 tracked, 14% of 14 non-tracked, $\chi^2=0.24$, df=1, p=0.62).

Movement patterns

Twenty-one males (excluding one unpaired male tracked for only 2.7h) were tracked for an average of 15.0±0.9h (range: 8.6-24.5h) and 196 OTMs were observed (Figure 3-1, Appendix 3-1). Of these trips 75% (147) involved silent intrusions onto the territory of at least one other male, whereas 25% of trips (49) involved movement into unoccupied habitat where males sang repeat songs which redstarts use to attract mates (Sherry and Holmes, 1997).

Off territory movements (OTMs)

Of three unpaired males, two SY males did not hold consistent territories throughout the breeding season and so their movements were not considered "off-territory" (see *Off-patch movements*). One unpaired ASY male held a territory in an unoccupied woodlot for the duration of the season, and made one OTM to unoccupied habitat. Paired males (n=19) moved off-territory at an average frequency of 0.8±0.1 OTM/h (range: 0.04-1.8 OTM/h). OTMs had a mean duration of 17±2 min/trip (range: 1-110 min/trip) and males spent an average of 18.2±0.03 % of their time off-territory (range: 0.2-51.5%). Eighty-six percent of trips lasted less than 30 min, but 9 males made 12 trips longer than 60 min. Mean trip distance was 103.5±10.4m, the maximum distance a paired male moved off his territory was 1167m, but 90% and 98% of trips were within 200m and 500m respectively. Of 205 observed intrusions, 77% were onto adjacent territories, 18% were to non-adjacent territories within the same breeding cluster, and 5% were to territories outside the breeding cluster. No paired males moved off-patch. Based on the availability of females at each breeding stage, territory intrusion was not directed randomly ($\chi^2=30.06$, df=3, $p<0.001$); males intruded onto territories of nest building females more often than expected and onto territories of laying, incubating and nestling-attending females less often than expected (Figure 3-2).

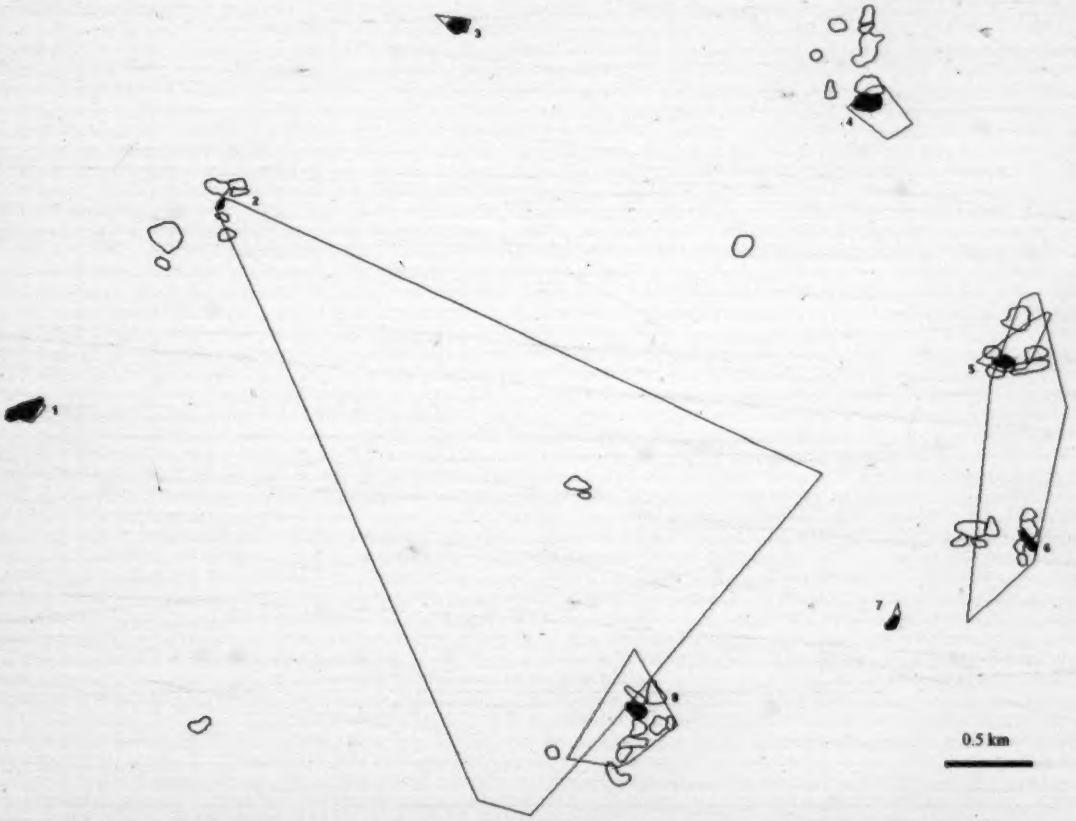

Figure 3-1. Activity spaces for eight males tracked in 2003. Grey polygons represent activity space, black polygons are territories of the tracked male, white polygons are territories of all other males in the landscape, grey areas are forest and white is open habitat including fields, roads and anthropogenic features. Activity spaces of unpaired males are represented by 2 and 3. Since activity spaces are minimum convex polygons around all tracking locations, territories that fall within activity spaces are not necessarily territories known to be visited by tracked males.

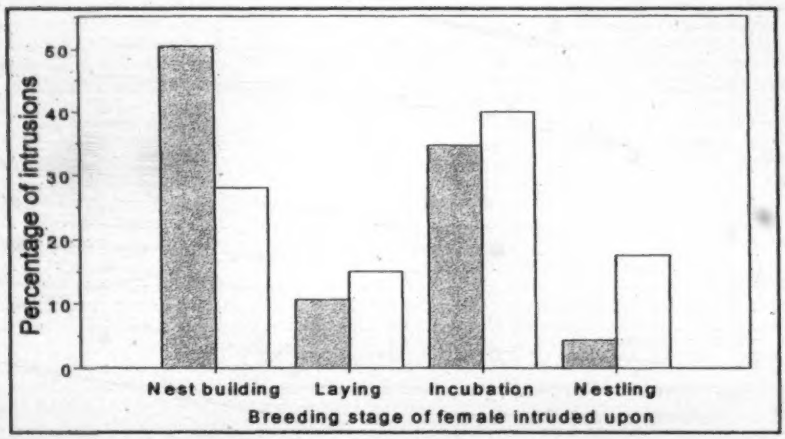

Figure 3-2. Percentage of intrusions onto the territory of females at each breeding stage. Grey bars are observed values and white bars are expected values based on the proportion of extra-pair females at each stage across the tracking period of all males.

Compared to expected values based on the average population age ratio across years, and based on all intrusions onto breeding-pair territories, intrusions were equally likely to be directed to SY and ASY females, (χ^2=2.39, v=1, p=0.12; mean percent ASY females in population=0.73). Although ASY males did not intrude onto territories of young and old males at a frequency different than expected (mean percent ASY males in population=0.70; χ^2=1.35, v=1, p=0.25), there was a trend for SY males to intrude more frequently onto territories of other SY males and less frequently onto territories of ASY males than expected (χ^2=3.21, v=1, p=0.07; Figure 3-3).

Paired males who left their territories frequently also had high intrusion frequencies (r=0.89, n=19, p<0.01) and a high percent time off-territory (r=0.86, n=19, p<0.01).

Off-cluster movements

Six of 19 paired males (5 ASYs) made a total of 12 off-cluster movements during tracking sessions. Males that moved off-cluster showed a trend of having closer nearest clusters ($\bar{x}$=328.0±52.7m, n=6) than did males not moving off-cluster ($\bar{x}$=551.7±115.7m, n=13; t=1.76, df=16, p=0.10). Four of 6 males increased their territory-intrusion counts by visiting other clusters.

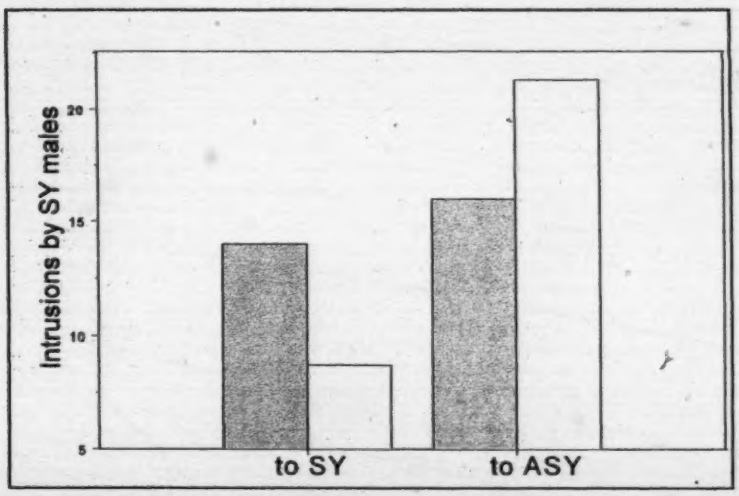

Figure 3-3. Intrusions by SY males onto territories of SY and ASY males. Grey bars indicate observed values, white bars indicate expected values based on the average proportion of males of each age class in the population across years (mean percent ASY males in population=0.70).

Off-patch movements

Two males made off-patch movements during tracking sessions. In 2003, one unpaired SY male held a singing territory for about two weeks then roamed across the landscape for the rest of the tracking period (male 2, Figure 3-1). In 2004, an unpaired SY male held a singing territory for a few days, was located 1.5km away and then not found again (despite searching within a 5km radius).

Correlates of movement investment (paired males)

Temporal factors: Time of day and breeding stage and season

OTM frequency, intrusion frequency and percent-time off-territory did not differ by time of day a male was tracked (Appendix 3-4). Similarly, OTM frequency and intrusion frequency did not differ across breeding stages, although males spent a lower percentage of their time off-territory in the nest-building stage relative to the laying and incubation stages (Appendix 3-4). Since most comparisons did not show statistical differences, tracking sessions across time-categories and breeding stages were pooled.

Female fertility was initially highly synchronous in both years showing peaks in early June and then declining, with an average of 35% of 38 and 29% of 26 females fertile per day during the tracking period in 2003 and 2004, respectively. In both years, the number of fertile females in the population declined significantly over the tracking

period (2003: r=-0.92, n_{days}=26, p<0.01; 2004: r=-0.74, n_{days}=36, p<0.01). However, the time of the season a male was tracked (male mean tracking date, years pooled) was not significantly correlated with OTM frequency (r=-0.25, n=19, p=0.29), intrusion frequency (r=-0.27, n=19, p=0.25), or percent time off-territory (r=-0.11, n=19, p=0.64).

Attributes of males, potential extra-pair mates and the landscape

OTM frequency was best predicted at the 500m scale (R^2=0.78; Table 3-1): older monogamous males in better body condition left their territories most frequently, and left slightly more frequently in 2004 than in 2003 (Table 3-1). Also, males in territories in areas of high forest cover, and lower synchrony during the tracking session left their territories more frequently (Table 3-1). The 200m-scale interaction model explained a similar amount of variation as the 500m-scale model (R^2=0.75): older monogamous males in areas of high local forest cover with many local females left their territories more frequently (Table 3-1). Also, males in areas of high local forest cover but fewer local females left their territories frequently.

Intrusion frequency was best predicted by the 200m-scale interaction model (R^2=0.71): males with high song investment, many local females and in areas of high local forest cover had the highest intrusion frequencies. Also, males in areas of high local forest cover, but fewer local females had high intrusion frequencies (Table 3-1).

Percent time off-territory was best predicted at the 500m scale (R^2=0.75): older monogamous males in better body condition spent the highest percentage of their time off-territory, and spent slightly more time off in 2004 than in 2003 (Table 3-1). Also, males with territories in areas of higher forest cover, with fewer females within 500m and lower synchrony spent a high percentage of their time off-territory (Table 3-1). The 200m-scale interaction model explained nearly as much variation (R^2=0.66): males with high song investment, with many local females, low synchrony and in areas of high local forest cover spent a high percentage of their time off-territory. Also, males in areas with high forest cover, but fewer females spent a high percentage of their time off-territory (Table 3-1).

Table 3-1. Multiple linear regression models for male OTM frequency, intrusion frequency and percent time off-territory. Stepwise parameter selection (*step* function in S-Plus) was conducted on global models including variables at the 200m and 500m scales[a]. Models containing retained terms are shown. Adjusted R^2 was increased by adding an interaction between density and forest cover to the retained 200m models only (shown below).

	scale	Model terms	Standardized coefficients, β[c]	p-value	F (df)	Model p-value	R^2	Adjusted R^2
OTMs/hr	200m	Status	-0.07	0.03	4.20 (3,15)	0.01	0.46	0.38
		Minimum Age	+0.07	0.02				
		Forest cover	+0.31	0.63				
	200m (interaction)	Status	-0.04	0.01	7.60 (5,13)	<0.01	0.75	0.64
		Minimum Age	+0.04	0.01				
		Forest cover	+2.30	0.03				
		Density	+0.15	<0.01				
		Forest cover x density	-0.19	0.01				
	500m	Year	+0.03	0.05	6.62 (6,11)	<0.01	0.78	0.65
		Status	-0.06	<0.01				
		Minimum Age	+0.12	<0.01				
		BCI	+0.08	0.13				
		Synchrony	-3.36	0.15				
		Forest cover	+2.36	0.02				
Intrusions/hr[b]	200m	Song investment	+1.32	0.06	12.00(2,16)	<0.01	0.60	0.55
		Density	+0.02	<0.01				
	200m (interaction)	Song investment	+0.40	0.12	8.64 (4,14)	<0.01	0.71	0.62
		Density	+0.11	0.01				
		Forest cover	+1.34	0.14				
		Forest cover x density	-0.13	0.04				
	500m	Song investment	+1.13	0.02	9.22 (2,16)	<0.01	0.54	0.47
		Forest cover	+1.53	0.02				
Percent time off-territory	200m	Song investment	+0.56	0.05	1.96 (3,15)	0.16	0.28	0.13
		Synchrony	-0.17	0.67				
		Forest cover	+0.11	0.64				
	200m (interaction)	Song investment	+0.34	0.02	5.12 (5,13)	0.01	0.66	0.52
		Synchrony	-0.80	0.07				
		Forest cover	+0.90	0.02				
		Density	+0.06	<0.01				
		Forest cover x density	-0.08	<0.01				
	500m	Year	+0.02	<0.01	4.24 (7,10)	0.02	0.75	0.55
		Status	-0.02	<0.01				
		Minimum age	+0.03	<0.01				
		BCI	+0.04	0.03				
		Density	-0.002	0.03				
		Synchrony	-1.12	0.09				
		Forest cover	+1.17	<0.01				

[a] Two global models were run for each dependent variable:
1) year+song investment+age+BCI+status+density200+synchrony200+forest cover 200, and
2) year+song investment+age+BCI+status+density500+synchrony500+forest cover500
[b] log-transformed to: log (1+intrusions/hr)
[c] Standardized coefficients (β) calculated as $SE_x/SE_y * b$, where b= term coefficient.

Movement and fertilization success

In 2003, 27% of chicks were extra-pair and 56% of broods contained at least one extra-pair chick (Chapter 2). In 2004, only 6% of chicks were extra-pair and 15% of broods contained at least one extra-pair chick (Chapter 2). Only 1 of 22 tracked males achieved an EPF. There was no difference in the proportion of tracked and non-tracked males that achieved EPFs (2003: 13% of 8 tracked males, 37% of 43 non-tracked males; proportions test: χ^2=0.91, df=1, p=0.34; 2004: 0% of 14 tracked males, 17% of 12 non-tracked males; proportions test: χ^2=0.54, df=1, p=0.46). The tracked male that achieved an EPF was an unpaired SY male in 2003 (male 2, Figure 3-1). Based on the fertile period of the extra-pair mate, he achieved the EPF before he abandoned his initial singing territory to roam across the landscape. The likelihood of being cuckolded was not related to OTM frequency (t=0.21, $n_{not\text{-}cuckolded}$=9, $n_{cuckolded}$=6, p=0.84), intrusion frequency (t=0.39, $n_{not\text{-}cuckolded}$=9, $n_{cuckolded}$=6, p=0.70) or percent time off-territory (t=0.51, $n_{not\text{-}cuckolded}$=9, $n_{cuckolded}$=6, p=0.62). There was no difference in the proportion of tracked and non-tracked males that were cuckolded (2003: 67% of 6 tracked males, 59% of 29 non-tracked males, proportions test: χ^2=0.13, df=1, p=0.71; 2004: 22% of 9 tracked males, 0% of 8 non-tracked males; proportions test: χ^2=0.44, df=1, p=0.51).

Discussion

Why move?

For paired male redstarts, OTMs appear to be primarily geared towards seeking additional fertilizations, whether through additional pair bonds or via EPFs; about 85% of all OTMs involved either intrusions or off-territory song. Moving males seem to have been primarily seeking EPFs: OTM frequency was highly correlated with intrusion frequency, with 75% of OTMs involving intrusions, and males intruded mostly onto territories of nest-building (fertile) females. Males also appeared to be seeking additional mates (polygyny) as 25% of OTMs were for off-territory singing trips in unoccupied habitat, where males sang repeat songs used primarily to attract females (Sherry and Holmes, 1997). However, although three of 19 tracked males in 2004 succeeded in obtaining a second mate, only one male during the study period achieved an EPF. I

suggest that the purpose of male movement is to obtain EPFs and polygyny, and give a number of reasons why so few moving males achieved EPFs.

When to move?

Time of day, season, breeding stage and synchrony

Time of day did not influence movement investment or intrusion rate, consistent with other studies (e.g. Stutchbury, 1998; Hanski, 1992) suggesting that EPCs may be equally likely at all times of the day. However, our tracking sessions did not encompass early evening, when redstart females may also be receptive to copulation attempts (Ficken, 1963).

OTM frequency and intrusion frequency did not differ across the season similar to Hooded Warblers (*Wilsonia citrina*; Stutchbury 1997), but males spent the least amount of time off-territory when their mate was most fertile (nest-building) and when breeding synchrony was high. In the early part of the season, when breeding synchrony is high males may face a trade-off between guarding their mates (and thereby protecting within-pair fertilizations) and seeking EPFs (Westneat et al., 1990). Although redstart males spend less time off-territory at this time, they still intrude frequently onto other territories via shorter-duration trips. Later in the season, when their mate is no longer fertile, males spend more time off-territory and make frequent OTMs and intrusions. Although fewer females are fertile at this stage of the season, OTMs and intrusions may still be fruitful for multiple reasons. High nest failure in this landscape (Hannon, unpublished) means that some females may be fertile at any stage of the season; re-nesting females may solicit EPCs and may move and seek different mates. Correspondingly, males with later nests are more frequently cuckolded than males with early nests (Chapter 2), and females have been observed switching mates following first-nest failure (Hannon, unpublished). Males also may move and intrude to acquire public information to assess the fertility status of extra-pair females, or their reproductive success to evaluate habitat quality in other areas of the landscape (Doligez et al, 2002).

Who moves?

Male status and quality (body condition, age and song)

Monogamous males were more likely to leave their territories than polygynous males, likely reflecting higher time and energy demands for polygynous males defending and moving between two territories. Accordingly, only one polygynous male from 2002 to 2005 achieved an EPF (Chapter 2). Although polygyny can accrue double the annual fertilization success of some monogamous males (Chapter 2), the likelihood of achieving a second mate is low (about an 11% polygyny rate from 2002 to 2005, Chapter 2) which likely explains why males invest more in seeking EPFs (i.e. via intrusions) than in off-territory song. Similar to another redstart population (Secunda and Sherry, 1991) polygyny was most frequent by ASY males in low-breeding-density years with higher proportions of SY males (Chapter 2). Under these conditions ASY males may be able to out-compete SY males for high-quality second territories (Secunda and Sherry, 1991).

Older males in good condition with high song investment invested most highly in movement. Although many paternity studies show age effects on EPF success (e.g. Perreault et al., 1997), this is one of few studies to date to show an age effect on OTM investment. That SY redstart males move less and are less likely to intrude on territories of ASY males, suggests that they are less likely to achieve EPFs than ASYs. This is corroborated in that ASY males are almost always sires of extra-pair young (Chapter 2). Similarly, old Reed Bunting (*Emberiza schoeniclus*) males have higher OTM frequencies than young males and achieve a greater number of EPFs (Kleven et al., 2005).

Although age was an important predictor of OTM frequency, song was a better predictor of intrusion frequency. Whereas male age may predict male quality, it is a fixed signal that does not reflect current condition. Song investment should be a better predictor since it is expensive and therefore an honest signal of real-time condition (Nowicki et al., 2000). Signals that reflect current condition, such as song and plumage qualities should be highly important since female assessment and choice of extra-pair mates is likely an ongoing process throughout the season (Safran et al., 2005). One major predictor of song investment is food availability (Alatalo, 1990, Gottlander, 1987), so male song may also reflect habitat quality and a thorough analysis of territory-level habitat quality would be needed to adequately assess this.

Access to and availability of extra-pair mates: density and forest cover

Males with greater availability of and access to extra-pair mates moved more extensively. Males left their territories and intruded more frequently when they were surrounded by many local (200m) females. High local density therefore increases encounters between possible extra-pair mates, and also likely improves a female's ability to detect and choose a high-quality extra-pair mate (Sullivan, 1994). Correspondingly, males with more local females are more likely to achieve EPFs (Chapter 2). Males spent more time off-territory when they had more females within 200m, but fewer females within 500m. It is possible that males with some immediate neighbours, but few beyond this, may spend more time searching or singing off-territory beyond their neighbours. However, density was not a strong predictor of time spent off-territory (i.e. low relative coefficient value).

Males in more highly forested areas left their territories more frequently, intruded on more females and spent more time off-territory. High forest cover also increased movement investment when density was low (*forest cover x density* interactions). Therefore, although high local density increases movement and intrusion rates, when local density is low and the local landscape is forested males may leave territories and spend high amounts of time off-territory in search of mates. Therefore, forest cover seems to increase the functional connectivity of this landscape. Males that visited other clusters also had closer nearest clusters, suggesting that dispersion of breeding clusters influences the likelihood of long distance movements. However, closer clusters were also more often connected by forest, so it is not clear whether distance between clusters or forest cover is more important for functional connectivity. Likely both are important and more study is needed here. Similarly, paternity analyses showed that males in isolated clusters (low forest cover, few neighbours) did not achieve EPFs and were cuckolded as frequently as males in non-isolated clusters (Chapter 2). Therefore, isolated clusters should be the lowest quality in terms of availability and access to extra-pair mates. This should be an important factor in settlement decisions by males who invest highly in the pursuit of additional mates (Norris and Stutchbury, 2001; Birkhead and Møller, 1992).

Why moving males did not achieve extra-pair fertilizations

Low detection probability?

Given the proportion of non-tracked males achieving EPFs in each year, I would have expected about two tracked males in each year to have achieved an EPF. So, it is not surprising that overall only one tracked male achieved an EPF. Therefore the lack of relationship between movement and EPF success may simply reflect low sample size and low population-level extra-pair paternity rates. However, in both years, males spent nearly 20% of their time off-territory and frequently intruded on territories of fertile females, so this still leaves the question as to why male movement did not increase fertilization success in these two years.

Do radio-transmitters influence mate choice?

Radio-transmitters did not statistically affect within-pair or EPF success but could potentially influence female perception of male extra-pair mate quality. In Zebra Finches (*Taeniopygia guttata*), leg-band colour is known to influence mate choice and males with preferred colour of bands have higher rates of unforced copulations with mates, their mates seek EPCs less frequently and they achieve higher fertilization success (Burley et al., 1994). If females are assessing quality of males among a pool of numerous candidates (Sullivan 1994), subtle differences in movement behaviour or appearance caused by radios could alter the likelihood that a male achieves an EPC or EPF. Although this should not affect comparisons among tracked males, it may reduce or preclude our ability to detect EPFs by tracked males and may underestimate the importance of male movement. Interestingly, three studies to date using transmitters have found that tracked males rarely or never gain EPFs (Stutchbury et al, 2005; Woolfenden et al., 2005, and this study), whereas a purely observational study of OTMs found a strong positive relationship between movement and EPF success (Kleven et al., 2005). It is difficult to assess the effect of radios given so few studies to date, and interspecies differences, but is essential to test this in order to fully understand the relationship between movement and EPF success.

Female behaviour and mate choice

Female movement and mate choice may be more important than male movement in determining male fertilization success (Stutchbury et al., 2005). Females move off-

territory in many species (reviewed in Griffith et al., 2002) and, in some species including redstarts, attract males using solicitation chips (Stutchbury, 1998, Ficken, 1963). Females can also influence sperm competition with post-copulatory mechanisms (Birkhead and Møller, 1992) and so persistently intruding and potentially copulating extra-pair males may not achieve EPFs if the male is not preferred. Redstart female movement and EPC behaviour has not been well documented so it is unclear what role females play in extra-pair matings. However, even if redstart females control extra-pair matings, they prefer high quality extra-pair males (Perreault et al., 1997, Kappes, 2004) and so the hypothesis of exclusive female control over EPFs is not consistent with high quality males investing most highly in movement. Similarly, Stutchbury et al. (2005) suggested that male attributes such as song and physical traits may correlate better with male EPF success in Hooded Warblers, however, redstart males with higher song investment and better body condition invest most in movement, so highly moving males should also be expected to achieve EPFs.

Is the benefit of movement density-dependent?

The benefits of movement in achieving EPFs may be density-dependent (Kokko and Rankin, 2006). Increased density increases EPF rates for many species (reviewed by Westneat and Stewart, 2003), and in our study redstart female density was an important predictor of intrusion frequency. Furthermore, there was a positive relationship between density and EPP within and across years in the study landscape (Chapter 2). Low density could reduce the number of encounters between females and extra-pair males (Westneat and Sherman, 1997). Even though males had similar intrusion frequencies in each year, a reduced number of males overall reduces the number of intrusions on each female. With fewer intrusions females may have a reduced ability to compare males and thereby have lower confidence in relative mate quality and so do not risk mating with a male other than her mate (Kokko and Rankin, 2006). Therefore, although males may move extensively in low density years for EPFs, if females are choosier, the benefit-to-cost ratio of male movement will be lower.

Why the relationship between movement and EPF success should not be ruled out

Patterns of EPF success corroborate movement patterns

Although movement did not translate into EPF success for tracked males, paternity patterns of non-tracked males in these study years reflect movement patterns (Chapter 2). The majority of extra-pair sires were ASY males, and were an average of 200m from their extra-pair young. Similarly, only males in higher-breeding-density clusters achieved EPFs. Although song investment was not assessed for non-tracked males, the tracked male with the highest song investment in 2004, secured the highest number of EPFs (4) in 2003 as a non-tracked male.

Movement and lifetime fertilization success

The benefit of extensive movement by paired males in this landscape should only be viewed in light of lifetime fertilization success. Males may not need to achieve an EPF in each year for movement benefits to outweigh costs. Furthermore, primary-nest failure in some years may increase the relative benefit of EPFs to total fertilization success, since 60% of males without successful nests achieved some reproductive success (Chapter 2; Perreault et al., 1997). Polygyny in one year could potentially match the contribution of EPFs across a male's lifespan. Overall, failure to find that extensively-moving males gain no EPFs in one study season (or even two) should not negate the importance of male movement as a mechanism for achieving EPFs and increasing lifetime fertilization success.

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Chapter 4: General Discussion

Future study

Reproductive costs and benefits of settlement choices

Measuring fertilization success from nestlings at day six post-hatch may not fully represent the reproductive costs and benefits to males of settling in isolated and non-isolated clusters. Nest failure from predation or brood parasitism by brown-headed cowbirds (which may be more frequent in larger clusters; Hannon, unpublished) may increase breeding-season energy expenditure, reduce clutch size (which is lower for re-nesting pairs; Hannon, unpublished), reduce fledging success or potentially delay migration to wintering grounds. If food availability is lower in isolated clusters, offspring may fledge in poorer condition and have lower survivability. Food quality and availability may best be assessed by Lepidoptera larvae abundance which likely comprises the majority of calories received by nestlings (unpublished provisioning data). Since movement and breeding density are lower in isolated clusters, these males also have a lower likelihood of being polygynous. These additional factors should be examined in order to thoroughly assess habitat quality and predict male settlement decisions.

Functional connectivity

Males in highly forested areas with closer neighbouring clusters moved the most and were most likely to visit other clusters. However, it is unclear whether proximity of neighbouring clusters or the presence of forested habitat between clusters is most conducive to movement. This could be tested in fragmented landscapes where males, or females, have the option to visit equally distanced clusters either within the same woodlot or across gaps of varying sizes. Cluster-intrusion frequencies could be assessed by radio-telemetry or mist-netting at cluster edges (Yezerinac and Weatherhead, 1997). It would be important to control for differences in male quality, since functional connectivity may differ depending on age or body condition. Furthermore, although in this study isolated males did not leave their forest patches, in higher-breeding-density years higher-quality males forced to settle in isolated patches might be able to compensate for isolation by crossing gaps or using corridors.

Female movement behaviour and mate choice

It is necessary to understand the role of redstart females in fertilization success. In this population few redstart copulations are observed which suggests that males do not frequently attempt forced copulations and that copulations are infrequent (apparently one or two pair-copulations per season; Ficken, 1963). Females also move off-territory and give solicitation chips which attract males (personal observations and Ficken, 1963). This suggests that female behaviour and mate choice is also important in determining fertilization success. Simultaneous tracking of both members of a pair (using two observers) may help to understand conflicts of interest between the sexes (Petrie and Kempenaers, 1998). Redstart females are difficult to catch until they have initiated a nest however, artificially inducing nest-failure could enable observations during the nest-building stage (when most sexual activity occurs; Ficken, 1963). Alternatively, without using radio-transmitters, observations of females when their mates are off-territory would also be beneficial. Future studies should also consider male plumage reflectance and song rate which may be most indicative of male quality. Nest location within the territory may also influence the likelihood of cuckoldry by neighbours (Westneat and Mays, 2005). A preliminary analysis of nest locations in 2003 and 2004 showed that nests were not closer to territory edges than expected by chance, but that 60% of nests are within 10m of the territory edge. Nests closer to specific neighbours may facilitate intrusions by specific males, may allow females to better assess quality of specific males or reduce the cost of female movement onto his territory.

The influence of radio-transmitters on mate choice

In order to understand the role of males in EPF success, using telemetry studies, it is essential to determine whether radio-transmitters influence male display ability and female mate choice. A number of studies suggest that radio-transmitters do not affect male behaviour (Stutchbury, 1998; this study), and in this study radios did not statistically reduce fertilization success. In future studies, a more rigorous comparison of the effects of radios on male display ability (e.g. plumage condition and reflectance, or sexual display postures) should be conducted. Female behaviour towards males with and without radios could be examined, such as response to male approaches or mounting attempts (e.g. acceptance or rejection rates), or frequency of solicitation chips when the

male is present and absent from the territory. Additionally, pairing success of early arriving males with and without mock transmitters could be compared.

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Appendix 2-1. Territory distribution, cuckoldry and EPF success from 2003 to 2005

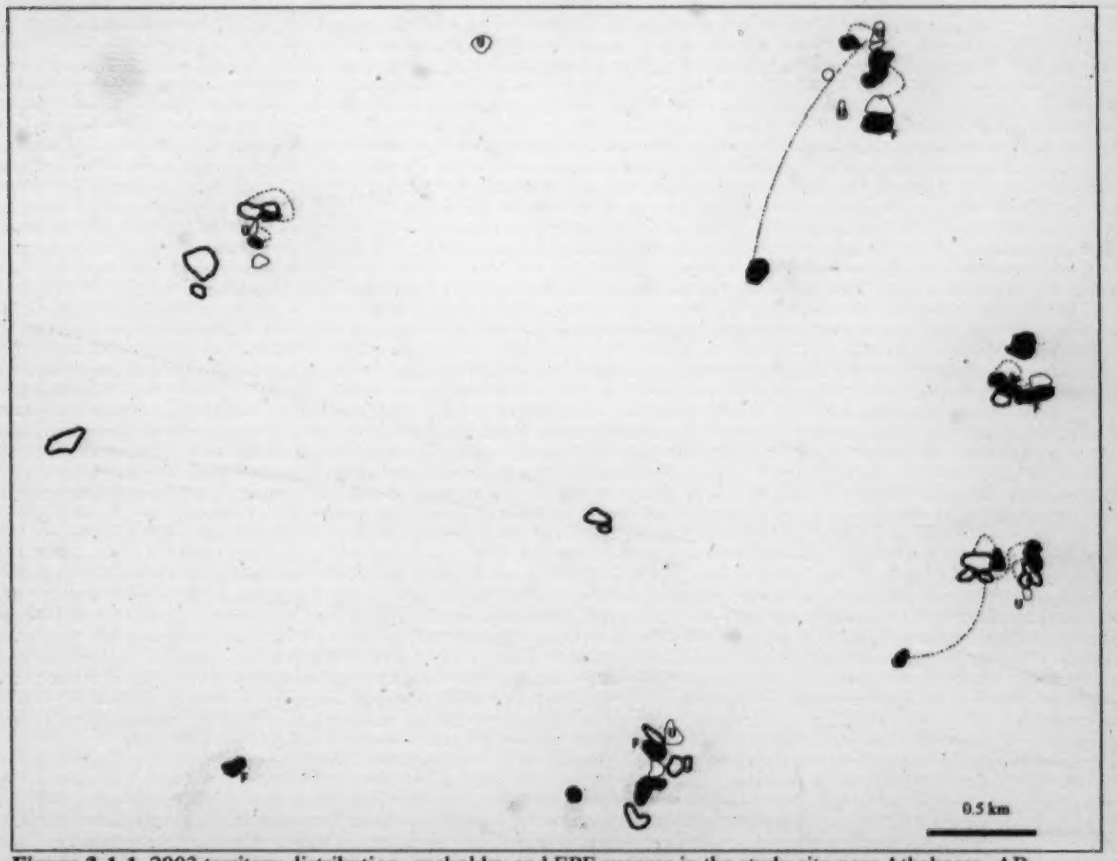

Figure 2-1-1. 2003 territory distribution, cuckoldry and EPF success in the study site near Athabasca, AB.. Light grey areas represent forest, white areas represent roads, fields and other non-habitat. Medium grey polygons represent occupied breeding clusters (see methods). White polygons represent territories of monogamous and unpaired ("U") males. Thick black lines encircle territories where offspring were sampled. Dark grey identifies territories of cuckolded males, and dashed lines extend to the identified sire (but do not represent movement trajectories). Where both males were cuckolded, an arrow leads from the identified sire to the cuckolded male. An "F" indicates where a male was cuckolded by an identified floater, resident unpaired or non-resident male.

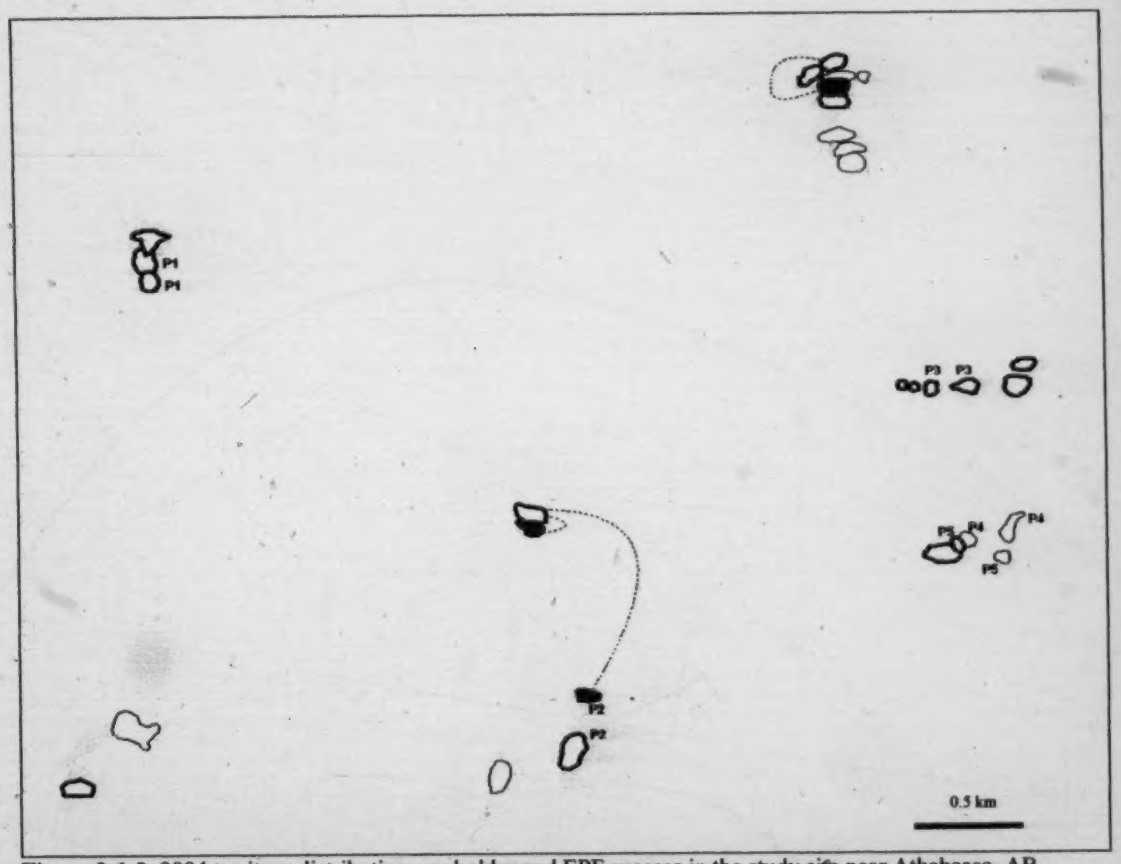

Figure 2-1-2. 2004 territory distribution, cuckoldry and EPF success in the study site near Athabasca, AB.. Light grey areas represent forest, white areas represent roads, fields and other non-habitat (note that forest above P3 was clear-cut prior to this breeding season). Medium grey polygons represent occupied breeding clusters (see methods). White polygons represent territories of monogamous and polygynous ("P_n" for each territory) males. Thick black lines encircle territories where offspring were sampled. Dark grey identifies territories of cuckolded males, and dashed lines extend to the identified sire (but do not represent movement trajectories).

Figure 2-1-3. 2005 territory distribution, cuckoldry and EPF success in the study site near Athabasca, AB.. Light grey areas represent forest, white areas represent roads, fields and other non-habitat. Medium grey polygons represent occupied breeding clusters (see methods). White polygons represent territories of monogamous and polygynous ("P_n" for each territory) males. Following nest failure, P3's second mate became P4's second mate. Both of P5's mates nested within the same territory. Thick black lines encircle territories where offspring were sampled. Dark grey identifies territories of cuckolded males, and dashed lines extend to the identified sire (but do not represent movement trajectories).

Appendix 2-2. Breeding Synchrony Indices

For cluster-level and population-level breeding synchrony, I used the standard breeding synchrony index of Kempenaers (1993):

$$SI = \frac{1}{F}\sum_{p=1}^{F}\left(\frac{\sum_{i=1}^{t_p} f_{i,p}}{t_p(F-1)}\right)\times 100$$

Where:
F = total number of breeding females a) within the cluster, or b) within the entire study population.
$f_{i,p}$ = number of fertile females (in the cluster or population), excluding female p, on day i
t_p = number of fertile days for female p

To calculate local breeding synchrony values for individual males, I used the abridged version from Yezerinac and Weatherhead (1997):

$$SI = \left[\frac{\sum_{i=1}^{t_p} f_{i,p}}{t_p(F-1)}\right]\times 100$$

Where:
F= the total number of females within a 200m radius
$f_{i,p}$ = number of fertile females (within 200m), excluding female p, on day i
t_p = number of fertile days for female p

Appendix 2-3. PCR reaction conditions and microsatellite characteristics

Table 2-3-1. Reaction conditions and thermal profiles for PCR amplification of microsatellites used in parentage analysis. All PCR was carried out in a 10μl reaction.

	locus		*Dpμ* 03	*Cuμ* 04	*Dpμ* 16	*Maμ* 23	*Dca* 28	*Dca* 32
Ingredients	water		3.9	3.8	1.9	4.3	1.4	1.4
	PCR buffer		1.0	1.0	1.0	1.0	1.0	1.0
	$MgCl_2$ (25mM)		1.0	1.0	1.5	0.6	1.5	1.5
	dNTPs (2mM)		2.0	2.0	4.0	2.0	4.0	4.0
	Forward primer (10μM)		0.5	0.5	0.25	0.5	0.5	0.5
	Reverse primer		0.5	0.5	0.25	0.5	0.5	0.5
	Taq polymerase (undiluted)		0.1	0.2	0.1	0.1	0.1	0.1
	DNA		1.0	1.0	1.0	1.0	1.0	1.0
Thermal profile	Initial denature (°C, min)		94,3	94,3	94,3	94,3	94,2	94,2
	30 cycles (°C, s)	denature	94,30	94,45	94,30	94,45	94,60	94,60
		anneal	57,30	51,45	57,30	55,45	46,60	46,60
		extension	72,30	72,45	72,30	72,45	72,45	72,45
	Final extension (°C, min)		72,5	72,5	72,5	72,5	72,20	72,20

Table 2-3-2. Characteristics of microsatellite loci for paternity analysis with 2004 and 2005 American redstart populations. Values were calculated from the adult population in each year.

Locus	Reference	Size range (bp)	Number of alleles	Heterozygosity $h_{observed}$	Heterozygosity $h_{expected}$	Exclusion probability (both parents known)	Null frequency
Dpμ 03	Dawson et al. (1997)	132-178	8	0.673	0.597	0.382	-0.0699
			10	0.667	0.635	0.423	-0.0371
Cuμ 04	Gibbs et al. (1999)	154-194	13	0.923	0.861	0.706	-0.0406
			10	0.821	0.864	0.707	0.0165
Dpμ 16	Dawson et al. (1997)	148-182	18	0.923	0.897	0.777	-0.0192
			15	0.919	0.888	0.755	-0.0273
Maμ 23	Alderson et al. (1999)	142-156	6	0.788	0.766	0.528	-0.0209
			5	0.821	0.758	0.515	-0.0549
Dca 28	Webster et al. (2001)	174-218	14	0.771	0.800	0.641	0.0156
			15	0.649	0.871	0.736	0.1480
Dca 32	Webster et al. (2001)	218-256	14	0.808	0.878	0.741	0.0382
			12	0.846	0.875	0.732	0.0110
Average							
2004			12.17			0.998[a]	
2005			11.17			0.999[a]	

note: no loci showed statistically significant heterozygote deficiencies (after a Bonferroni adjustment for multiple tests; adjusted α=0.002) based on the procedure by Rousset and Raymond (1995), calculated in *Cervus*.

[a] Average probability of paternal exclusion: the probability that a random non-sire male from the population will not possess the paternal allele found in the offspring, given that the maternal genotype is known.

Appendix 2-4. Weather conditions

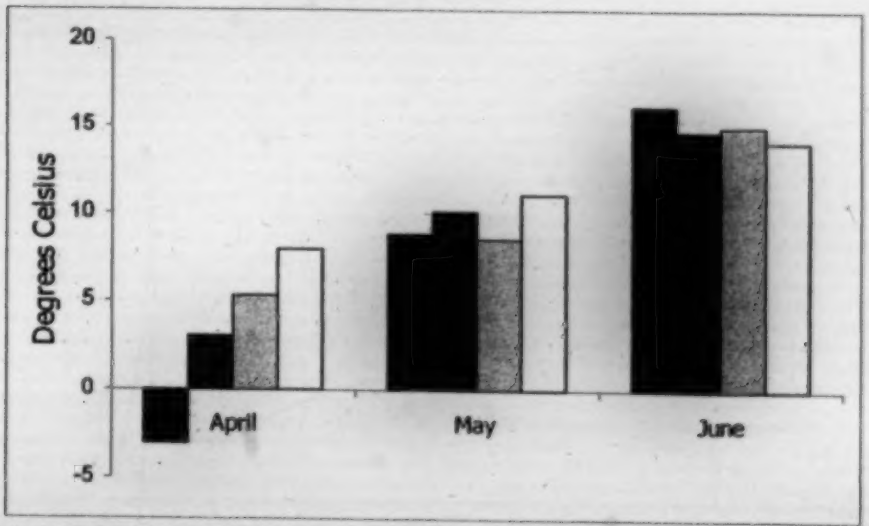

Figure 2-4-1. Mean monthly temperature (°C) before (April and May) and during (June) the peak nesting period of redstarts in the study landscape from 2002 through 2005 (black to white bars, respectively). Conditions were measured at the Colinton, Alberta weather station, approximately 4km NE of the study site (54°63'N, 113°22'W, elevation 602m). Data compiled from the Environment Canada National climate data and information Archive (www.climate.weatheroffice.gc.ca).

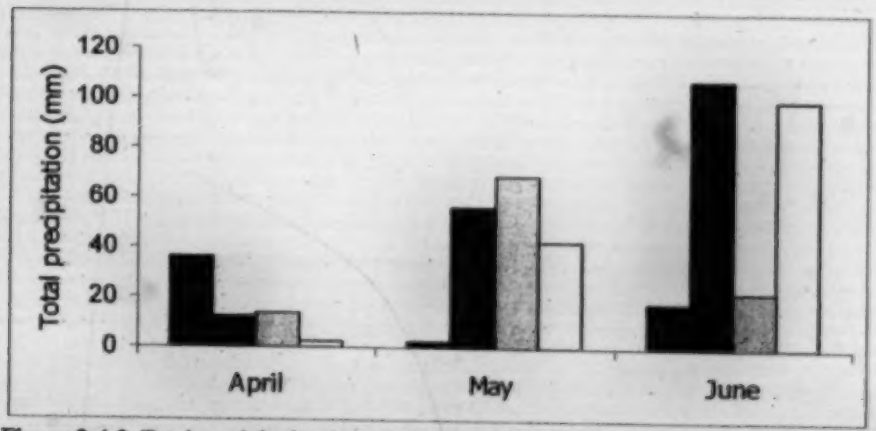

Figure 2-4-2. Total precipitation (mm) before (April and May) and during (June) the peak nesting period of redstarts in the study landscape from 2002 through 2005 (black to white bars respectively). Conditions were measured at the Colinton, Alberta weather station, approximately 4km NE of the study site (54°63'N, 113°22'W, elevation 602m). Data compiled from the Environment Canada National climate data and information Archive (www.climate.weatheroffice.gc.ca).

Appendix 2-5. "Synchrony" models of fertilization success

Table 2-5-1. "Synchrony" generalized linear models of cuckoldry and extra-pair fertilization success for individual males and within clusters for 2002 and 2003 redstart populations. Terms were removed using the *step* function in S-Plus. A rank of removal of 1 indicates the term was first to be removed in the stepwise process and no rank indicates a term was retained.

Model	Coefficients[a]	χ^2 (df_{sub}, $df_{residual}$)	p-value, direction of effect		Rank of removal	Percent deviance explained by full model (by reduced model)
Male- Cuckolded? (no, yes)[b]						
Year	136.71	0.43	0.51	+		49 (13)
DFE	0.16	6.02	0.01	+		
Arrival	0.88	4.15	0.04	+		
Year x arrival	0.95	1.96	0.16	-		
density	1.43	2.81	0.09	-		
Year x density	1.26	4.92	0.03	+		
synchrony	4.13	2.97	0.08	-		
Status		0.40	0.53	+	1	
Age		1.30	0.25	+	2	
density x synchrony		0.01	0.91	-	3	
BCI		0.43 (37, 26)	0.51	-	4	
Cluster- Proportion of males cuckolded[b]						
density	4.47	0.11	0.74	+		24 (13)
Forest cover	0.09	1.43	0.23	+		
density x forest cover	0.06	0.87	0.35	-		
density x synchrony		<0.01	0.93	-	1	
Year		0.01	0.91	+	2	
synchrony		2.96 (17,11)	0.09	+	3	
Male - EPF achieved? (no, yes)[b]						
Year	2.98	0.33	0.57	+		40 (11)
density	0.01	1.19	0.27	+		
Year x density	0.85	3.30	0.07	-		
synchrony	3.52	2.52	0.11	+		
Status		1.55	0.21	-	1	
Age		1.80	0.18	+	2	
Year x arrival		0.32	0.57	-	3	
density x synchrony		3.20	0.07	+	4	
Arrival		0.67	0.41	-	5	
BCI		1.84 (54,44)	0.17	-	6	
Cluster - Proportion of males achieving an EPF[b]						
density	14.57	0.26	0.61	+		61 (56)
synchrony	4.77	<0.01	0.95	-		
Forest cover	0.24	1.58	0.21	+		
density x forest cover	0.16	2.77	0.10	-		
density x synchrony		0.44	0.51	+	1	
Year		6.42 (17,11)	0.01	+	2	

[a] coefficients are from reduced models (containing only retained terms)

[b] *GLM with binomial errors*

Appendix 3-1. 2004 activity spaces and territory distribution

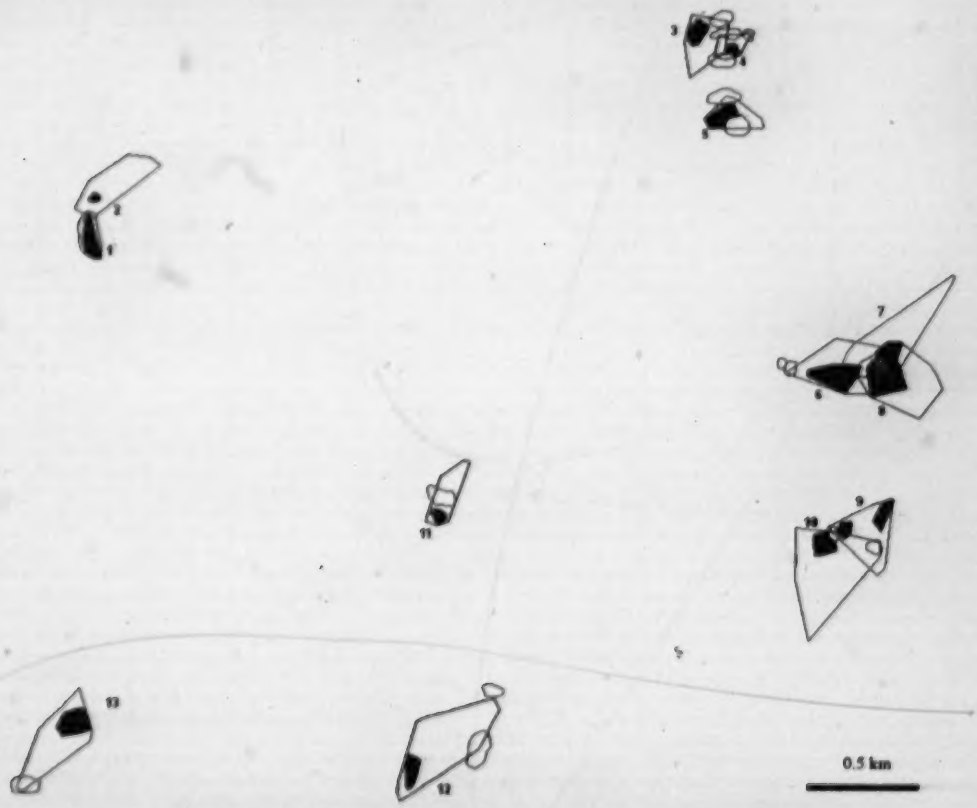

Figure 3-1-1. Activity spaces for 13 males tracked in 2004. Grey polygons represent activity spaces, black polygons are territories of the tracked male, white polygons are territories of all other males in the landscape, grey areas are forest and white is open habitat including fields roads and anthropogenic features. The activity space of one unpaired male who left the landscape is not shown. Males 1,6 and 9 were polygynous: male 1 and 6's second mates were in adjacent territories and male 9's mates were about 200m apart. In all three cases, males defended, by song, the area between mates. Since activity spaces are minimum convex polygons around all tracking locations, territories that fall within activity spaces are not necessarily territories known to be visited by tracked males.

Appendix 3-2. Radio-transmitter attachment and retrieval method

The radio attachment procedure of Raim (1978) was adapted for use by C. Gillies (University of Alberta), which was then further modified for use with Redstarts in this study. A lightweight-medium-weave piece of nylon material about 50% larger on all sides than the body of the LB-2N transmitter was glued with Instant KrazyGlue® to the back of the transmitter. It was allowed to dry for 1h, and then was trimmed so that its final size was about 10% larger on all sides than the transmitter body, to increase surface area for attachment to the bird. While a bird was still inside a capture bag, Ardell® LashGrip™ eyelash adhesive (American International Industries) was generously applied to the back of the nylon. This allowed the glue 2-3min to dry while the bird was removed from the bag and measured. This increased the stickiness of the glue and reduced the time a bird needed to be held. A patch of feathers on the spine between and about 1cm below the scapulae were lifted and held while 5 or 6 feathers were cut at their base to reveal a bare patch of skin slightly smaller than the nylon attached to the transmitter. The transmitter was then carefully positioned above the bare patch, and then moved into place, so as not to spread glue onto the feathers. Moderate pressure was applied to the back of the radio to ensure good contact between the skin, glue and nylon, while ensuring that the bird could adequately breathe. After 10 min, pressure was released and the radio was pulled gently to ensure it had dried in place. The held feathers were released, which fell back into place and completely covered the transmitter body. Different methods were tried at the beginning of the 2003 season, where feathers were not cut, were not cut to their base and where the bird was held for shorter time periods, but no method worked as well as this. Of radios attached with this method, only 1 transmitter in 2003 and 1 in 2004 fell off before the battery expired, after 15 and 12 days respectively. In both seasons, transmitter retrieval was attempted. I used surgical scissors to cut feather stubs between the nylon and the skin, allowing transmitters to be peeled away

Appendix 3-3. Error in bird locations

Uncorrected GPS points had a mean horizontal precision (i.e. radius) of 5.0m. Upon differential correction with Hinton, AB. base station files (TerraPro GPS Ltd.) mean horizontal precision was reduced to 2.01m. Therefore the location of each bird had a maximum error radius of about 4.5m.

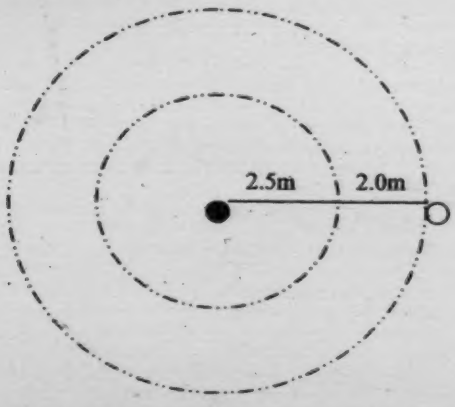

Figure 3-3-1. Error in bird locations. The black dot indicates the estimated location of the bird, the inner ring represents mean error in my estimation of the bird's position, and the outer ring represents the additive effect of mean GPS error. The white circle represents the maximum mean potential error in the assigned location.

Appendix 3-4. Spatial autocorrelation

Table 3-4-1. Moran's I and Getis-Ord General G tests for spatial autocorrelation in ArcGIS 9.0 with dependent movement investment variables at various threshold distances. Tests are with all paired tracked males (n=19), coordinates were taken from territory centroids, and euclidian distance was used for weight matrices.

Dependent variable	Threshold distance (m)	Moran's I[a]	p	Getis-Ord General G[b]	P
OTM/hr	0	-0.07	>0.1	<0.01	>0.1
	200	-0.16	>0.1	<0.01	>0.1
	500	-0.07	>0.1	<0.01	>0.1
Intrusions/hr	0	0.04	>0.1	<0.01	>0.1
	200	0.03	>0.1	<0.01	>0.1
	500	0.11	>0.1	<0.01	>0.1
Percent time off-territory	0	-0.03	>0.1	<0.01	>0.1
	200	-0.04	>0.1	<0.01	>0.1
	500	-0.04	>0.1	<0.01	>0.1

[a] Moran's I tests for global spatial autocorrelation. Values near -1 and + 1 indicate that across observations at a given threshold distance, nearer observations have dissimilar values (negative spatial autocorrelation) and similar values (positive spatial autocorrelation), respectively. With high p-values such as above, ArcGIS concludes that the "*pattern is neither clustered nor dispersed*" and could have arisen by random chance.

[b] The Getis-Ord General G test assesses whether "hot-spots" occur in the population where similar or dissimilar values are clustered. Similarly, high positive G values indicate spatial clustering of similar observations and low negative values indicate spatial clustering of dissimilar observations. With high p-values such as above, ArcGIS concludes that "*no apparent clustering is detected at this scale*" and the observed clustering could have arisen by random chance.

Appendix 3-5. Movement investment by breeding stage and tracking time-category

Table 3-5-1. OTM frequency, intrusion frequency and percent time off-territory for 19 paired males relative to breeding stage of the social mate and tracking time-category. Sample sizes in parentheses represent the number tracking sessions.

		OTM/hr	Test	Intrusions/hr	test	Percent time off-territory	test
Breeding stage	Nest-building (60)	0.66±0.11	[a]*H_3=4.98, p=0.17*	0.63±0.13	*H_3=1.51, p=0.68*	0.11±0.02	*H_3=11.68, p<0.01*
	Laying (26)	0.93±0.17		0.71±0.19		0.31±0.06	
	Incubating (72)	0.79±0.10		0.80±0.14		0.23±0.03	
	Nestling (11)	0.95±0.26		0.47±0.16		0.16±0.05	
Tracking time category	6h00-8h00 (48)	0.78±0.13	H_3=1.89, p=0.60	0.72±0.17	H_3=4.12, p=0.25	0.19±0.04	H_3=7.10, p=0.07
	8h00-10h00 (42)	0.80±0.11		0.85±0.15		0.22±0.04	
	10h00-12h00 (49)	0.74±0.15		0.61±0.15		0.14±0.03	
	14h00-16h00 (30)	0.79±0.12		0.61±0.15		0.27±0.05	

[a] Kruskal-Wallis test